

## Review of:

# Linking Sea–Air and Benthic Methane Fluxes Across Seasons in a Tropical Seagrass Meadow of Taiwan

The reviewed study investigates the methane production and release from seagrass meadows compared to water bodies with sandy sediments, examining diel, seasonal and annual variability. This is done using benthic chambers and porewater profiling in the Haikou seagrass meadow and adjacent bare sand habitats. Methane fluxes between sediment and water column, and atmospheric fluxes were estimated and compared using bulk models. The authors found that the seagrass meadow had stable methane emissions while sandy sediments were more variable. Additionally, the sediment-water flux was found to be considerably higher than the water-air flux.

## 1 General Assessment

The paper addresses relevant scientific questions within the scope of BG. It presents novel concepts and data and substantial conclusions are reached. The descriptions of experiments and calculations are sufficiently complete to allow reproduction and give proper credit to related work. The title reflects the content of the paper and the abstract provides a concise and complete summary. The overall presentation and structure is in general clear and the language is fluent and precise; however, the resolution of Figures 3-6 must be improved and Table 2 and 3 are currently somewhat messy and hard to read. Mathematical formulae, symbols, abbreviations and units are correctly defined and used; however, I would in general prefer to avoid using the letter “x” (or the saltire × for that matter) as multiplication sign. No parts of the paper need shortening, clarification, reduction, merging or elimination. The number and quality of references is appropriate. The amount and quality of supplementary material is sufficient (only their measured data).

I only have one major comment to the manuscript which relates to the application of methodology and interpretation of the atmospheric methane fluxes which is described below in its own section. Apart from that, the scientific methods and assumptions seems valid and clearly outlined and the results are sufficient to support the conclusions.

The manuscript is interesting, very easy to read and well written, and the scientific rigour seems solid. I enjoyed reading the paper and congratulate the authors on a nice piece of work. I recommend publication subject to revisions as indicated in the present review. I also support the opinions of Reviewer 1 and 2.

## 2 Main comment: Methane fluxes to the atmosphere

This comment mainly relates to section 2.4 and section 3.5 and associated sentences in the abstract and conclusion. There are several aspects of the reasoning here that are worth commenting on and both methodology, text and conclusions needs revision. The topic of this discussion concerns the relevance of the CH<sub>4</sub> emission estimate (78.3 moles) and associated reasoning and interpretation. I believe the current approach is quite irrelevant for evaluating the impact of the seabed released methane on the atmospheric methane budget and furthermore, that it considerably under-values this impact.

In this Section and elsewhere in this review, when referring to equation numbers, I refer to equations in this review and will explicitly state if I refer to equations in the published preprint.

### 2.1 The applicability of Wanninkhof (2014)

The water-air fluxes of methane is calculated using a bulk model presented in Wanninkhof (2014) using observed water column dissolved methane concentration and the atmospheric equilibrium concentration as input, i.e.

$$F_{\text{obs}} = \kappa(C_{\text{local}} - C_{\text{eq}}), \quad (1)$$

where  $F_{\text{obs}} > 0$  is the observed local sea-air methane flux (being a net contribution to atmospheric methane),  $C_{\text{obs}}$  is the locally observed water concentration, and  $\kappa$  is a gas-specific, temperature-dependent gas transfer coefficient function. This coefficient function is empirically determined and was originally developed and

tailored for global CO<sub>2</sub> estimates and carries an estimated uncertainty of approximately 20% even within its intended application. When applied to a local coastal region rather than an ocean basin and to a different gas, considerably greater uncertainties are expected. That being said, I am not aware of better models that can be applied using the available data and I do not think any methodological changes are needed here. I do, however, recommend adding a sentence to comment on this aspect.

## 2.2 Using equilibrium concentration in Eq. (1)

The surface water of the ocean is in general undersaturated on methane with respect to the atmosphere (i.e. *not* in equilibrium) and the ocean is a net sink of atmospheric methane. A reasonable assumption is therefore that the local sea-air contribution to atmospheric methane in *absence* of seabed methane sources would be

$$F_{\text{baseline}} = \kappa(C_{\text{baseline}} - C_{\text{eq}}), \quad (2)$$

where  $F_{\text{baseline}} < 0$  is the global sea-air methane flux (acting as a net sink of atmospheric methane) and  $C_{\text{baseline}}$  is the global or regional average surface water concentration (or average surface water in similar areas *without* seagrass).

A question then arises: What is the best way to describe the *local* atmospheric methane contribution from the area of interest (meadow, sandy, or coastal) using the observed water column methane concentration? I would argue that the correct way to approach this is to then calculate the *difference* between the observed local flux (Eq. (1)) and the baseline flux in absence of sources, i.e.

$$\Delta F = F_{\text{obs}} - F_{\text{baseline}} \quad (3)$$

where  $\Delta F$  is the net difference in atmospheric methane flux in the study area due to local production. Substituting in Eq. (1) and (2) we then get the following expression for the contribution from the local area (meadow, sandy seabed or coastal):

$$\Delta F = \kappa(C_{\text{obs}} - C_{\text{eq}}) - \kappa(C_{\text{baseline}} - C_{\text{eq}}), \quad (4)$$

which reduce to

$$\Delta F = \kappa(C_{\text{obs}} - C_{\text{baseline}}), \quad (5)$$

and consequently, the net *contribution* from the study area becomes  $\int \Delta F \cdot A_{\text{obs}} dt$ , where  $A_{\text{obs}}$  is the size of the study area.

I am not going to strictly suggest changing the methodology here - the emission estimate *is* indeed relevant when comparing to e.g. the sandy and coastal area, however, I think using  $C_{\text{eq}}$  at least requires a short discussion about what this really means and how it under-values the contribution from local production and. This is particularly important here since the context is the evaluation of climate mitigation efforts using seagrass meadows as carbon storages. In this context, if the aim is to quantify the *net* greenhouse effect of seagrass meadows, using  $C_{\text{eq}}$  will under-value the effect of local methane production. Even though the difference in  $C_{\text{baseline}}$  and  $C_{\text{eq}}$  is small, it will still yield a relatively large difference in estimates since the average concentration ( $C_{\text{obs}}$ ) is relatively low ( $\sim 8$  nmol/L).

## 2.3 Free gas release

The approach does not take into account free gas release via bubbles. At least not when quantifying atmospheric release. It is also not clear from reading the manuscript how prevalent bubble release is. In cold seep environments the majority of gas is released via bubbles. In such environments, with a 5 m water column, most of the gas would be released to the atmosphere as free gas via bubble transport and only a small fraction would be dissolved (McGinnis et al., 2006; Jansson et al., 2019). This should be commented on and if possible, at least qualitatively evaluated.

## 2.4 The fate of the dissolved methane

Another important (most likely the most important) aspect is missing here, namely a proper discussion on the final fate of the dissolved methane. In Line 248-250 it is stated that "*Benthic sediments in the Haikou seagrass meadow released approximately 1,410.1 mol CH<sub>4</sub> yr<sup>-1</sup> into the overlying seawater, whereas the water*

column emitted only about  $78.3 \text{ mol CH}_4 \text{ yr}^{-1}$  to the atmosphere.”, then in Line 253-255: “This imbalance between sediment production and atmospheric emission indicates that roughly 94% of sediment-derived  $\text{CH}_4$  was oxidized within the water column before reaching the atmosphere or being transported laterally.” While this is technically correct, I believe this strongly under-states how much of the laterally transported  $\text{CH}_4$  could be released to the atmosphere and/or contribute to the net atmospheric methane budget.

As shown in modelling studies by Nordham et al., (2025) and Dølven et al., (2025) a considerable amount of seabed released dissolved methane can be released to the atmosphere at a later stage. In both these studies, the cases discussed concerned situations where  $\text{CH}_4$  was released at depth, i.e.,  $\sim 70$  and  $\sim 250$  meter, respectively. Both these modelling studies highlights the water columns ability to suppress vertical exchange of water masses as an important factor for resulting atmospheric flux. In Nordham et al., (2025), which is closest to the present study with methane injection at 70 m depth, model estimates showed that 17-43% of dissolved methane will escape at some point in the future. In the present study, the methane is injected directly to surface water, which should facilitate considerably more efficient atmospheric exchange.

### 2.4.1 Quantifying atmospheric contributions

That the methane in this case is released directly into the well mixed surface layer makes this study particularly well suited for doing a simple estimate of of how much of the released methane will be released to the atmosphere and how much will be consumed by microbes. In fact, the exercise can be done analytically if one accepts some simple assumptions:

1. All methane is released directly into the surface water (as defined by Wanninkhof (2014)) and remains in a well mixed surface layer of the ocean in all foreseeable future.
2. Microbial oxidation (MOx) can be modeled using first order kinetics, i.e.,

$$L_{ox} = k_{ox} C_{obs}, \quad (6)$$

where  $L_{ox}$  is the volumetric loss rate ( $\text{mol m}^{-3} \text{ s}^{-1}$ ), and  $k_{ox}$  is the rate coefficient ( $\text{s}^{-1}$ ).

3. Added methane molecules ultimately are either:
  - physically escaping to the atmosphere via gas exchange, or
  - consumed by microbes.

In other words, all added methane that is *not* consumed will contribute to ocean-atmosphere exchange at some point.

We define the added methane molecules to the ocean, in this case from the seagrass meadow, as  $M_0$  and the evolution in time of that pool of methane molecules as  $M(t)$ . The mass  $M(t)$  is then distributed within a well-mixed surface layer of depth  $H$  and area  $A$ , thereby disturbing the surface layer concentration by

$$\frac{M(t)}{AH} = C(t) - C_{\text{baseline}}. \quad (7)$$

In practice,  $C(t)$  is just the time variant  $C_{\text{obs}}$  from Eq. (5), and by substituting  $\Delta F = \kappa(C_{\text{obs}} - C_{\text{baseline}})$  (from Eq. (5)) into Eq. (7) we obtain

$$\frac{M(t)}{AH} = \frac{\Delta F(t)}{\kappa} \Rightarrow \Delta F(t) \cdot A = \kappa \cdot \frac{M(t)}{H}. \quad (8)$$

This is simply the time varying mass contribution to the atmosphere caused by the added molecules (flux times area). We define this as

$$\Phi_{\text{atm}}(t) = k_{\text{atm}} M(t), \quad (9)$$

where  $\Phi_{\text{atm}}(t) = \Delta F(t) \cdot A$  represents the instantaneous atmospheric escape rate ( $\text{mol s}^{-1}$ ) and  $k_{\text{atm}} = \kappa/H$  ( $\text{s}^{-1}$ ) is an atmospheric escape rate coefficient.

The amount of methane consumed by microbes can be obtained by integrating Eq. (6) over the same volume and we get:

$$\Phi_{\text{ox}}(t) = L_{\text{ox}}(t) \cdot AH = k_{\text{ox}} C(t) \cdot AH \quad (10)$$

$$\Phi_{\text{ox}}(t) = k_{\text{ox}} M(t). \quad (11)$$

This represents the oxidation rate ( $\text{mol s}^{-1}$ ) for the added methane molecules and  $k_{\text{ox}}$  is the oxidation rate coefficient. Since all methane must either reach the atmosphere or be oxidized (assumption 3), and both processes follow first-order kinetics competing for the same pool, we can write the partitioning rates as:

$$\Phi_{\text{atm}}(t) = k_{\text{atm}}M(t) \quad (\text{rate committed to atmosphere}) \quad (12)$$

$$\Phi_{\text{ox}}(t) = k_{\text{ox}}M(t) \quad (\text{rate oxidized}), \quad (13)$$

and total depletion rate of the added methane pool is:

$$\frac{dM(t)}{dt} = -(\Phi_{\text{atm}} + \Phi_{\text{ox}}) = -(k_{\text{atm}} + k_{\text{ox}})M(t), \quad (14)$$

which when solved for  $M(t)$ , using the initial condition  $M(0) = M_0$  gives the temporal evolution of the mass of the added methane molecules

$$M(t) = M_0 e^{-(k_{\text{atm}} + k_{\text{ox}})t}. \quad (15)$$

We can obtain the total amount of the added methane that is committed to the atmosphere,  $M_{\text{atm}}^\infty$ , by substituting  $M(t)$  in Eq. (12) and integrate the atmospheric partition to infinity

$$M_{\text{atm}}^\infty = \int_0^\infty \Phi_{\text{atm}} dt = \int_0^\infty k_{\text{atm}}M(t) dt = k_{\text{atm}}M_0 \left[ e^{-\infty} + \frac{e^0}{k_{\text{atm}} + k_{\text{ox}}} \right] = \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} M_0 \quad (16)$$

and the total amount of oxidized methane,  $M_{\text{ox}}^\infty$ , becomes

$$M_{\text{ox}}^\infty = \int_0^\infty \Phi_{\text{ox}} dt = \int_0^\infty k_{\text{ox}}M(t) dt = k_{\text{ox}}M_0 \left[ e^{-\infty} + \frac{e^0}{k_{\text{atm}} + k_{\text{ox}}} \right] = \frac{k_{\text{ox}}}{k_{\text{atm}} + k_{\text{ox}}} M_0, \quad (17)$$

which together adds up to the initially released methane  $M_0$  as follows

$$M_{\text{atm}}^\infty + M_{\text{ox}}^\infty = \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} M_0 + \frac{k_{\text{ox}}}{k_{\text{atm}} + k_{\text{ox}}} M_0 = \frac{k_{\text{atm}} + k_{\text{ox}}}{k_{\text{atm}} + k_{\text{ox}}} M_0 = M_0. \quad (18)$$

The fraction of released methane that will contribute to air-sea exchange is then simply given by

$$f_{\text{atm}}^\infty = \frac{M_{\text{atm}}^\infty}{M_0} = \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} \cdot \frac{M_0}{M_0} = \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} \quad (19)$$

and fraction oxidised methane becomes

$$f_{\text{ox}}^\infty = \frac{M_0 - M_{\text{atm}}^\infty}{M_0} = 1 - \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} = \frac{k_{\text{atm}} + k_{\text{ox}}}{k_{\text{atm}} + k_{\text{ox}}} - \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} = \frac{k_{\text{ox}}}{k_{\text{atm}} + k_{\text{ox}}}. \quad (20)$$

In other words, the amount of released methane that contributes to the atmospheric methane budget is, under assumption 1-3, solely dependent on the ratio between the atmospheric escape rate coefficient  $k_{\text{atm}}$  and microbial oxidation rate coefficient  $k_{\text{ox}}$ .

Both  $k_{\text{atm}}$  and  $k_{\text{ox}}$  can vary considerably. Using an assumed average mixed layer depth of  $H = 100$  m (for the part of the ocean where the molecules will be distributed in their ocean residence time) and the global values from Wanninkhof of  $T = 20$  and a 10 m wind speed  $U_{10} = 7.3$   $\text{m s}^{-1}$ , we obtain a value for  $k_{\text{atm}} \approx 3.5 \cdot 10^{-7}$   $\text{s}^{-1}$ . Ranges for estimated  $k_{\text{ox}}$  values vary substantially, from days to years (e.g., Griffiths et al., 1982; Kessler et al., 2011; Leonte et al., 2017; Gründger et al., 2021) and a good understanding of the dynamics of methane oxidizing bacterial communities is lacking, for instance how reaction rates change with concentration. There seems to be a tendency, however, for lower reaction rates in areas with lower methane concentration. Using a mid-range value from Table E1 in Dølven et al. (2025) where several  $k_{\text{ox}}$  values are summarized, we assume a  $k_{\text{ox}}$  of  $10^{-7}$   $\text{s}^{-1}$ . The fractional contribution to atmosphere-ocean exchange  $f_{\text{atm}}^M$  then becomes

$$f_{\text{atm}}^M = \frac{k_{\text{atm}}}{k_{\text{atm}} + k_{\text{ox}}} = \frac{3.5 \cdot 10^{-7}}{3.5 \cdot 10^{-7} + 10^{-8}} \approx 0.77. \quad (21)$$

Thus, with these assumed values and assumptions,  $\approx 77\%$  of the methane released to the surface layer will contribute to the atmospheric methane budget. However, the potential range depends entirely on the assumed values for the largely unconstrained values for  $k_{\text{atm}}$  and  $k_{\text{ox}}$ . Figure 1 illustrates this range where measured

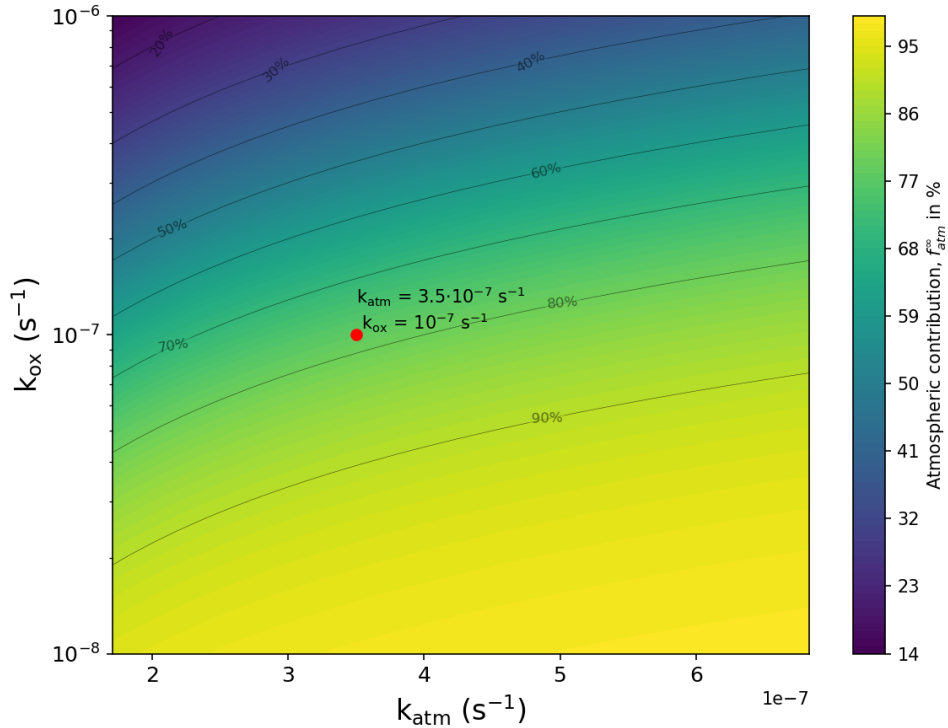


Figure 1: Fractional (percentage) loss of methane to the atmosphere from the added pool of methane molecules as a function of the microbial oxidation rate coefficient ( $k_{\text{ox}}$ ) and the sea to air mass loss rate coefficient ( $k_{\text{atm}}$ ). The y-axis is plotted using a log-scale.

and/or calculated ranges for oxidation rate coefficients have been used - specifically  $f_{\text{atm}}^{\infty}$  have been calculated for the range  $10^{-8} \leq k_{\text{ox}} \leq 10^{-6} \text{ s}^{-1}$  based on Table E in Dølven et al. (2025) and  $k_{\text{atm}}$  have been calculated for wind speeds ranging from 5 to 10  $\text{m s}^{-1}$  and mixed layer depths from 50 to 150 m.

Even though the estimate has large uncertainties and is highly dependent on assumed rate coefficient values, it highlights that of the 94% of sediment-derived methane that is laterally advected away from the local area, it is likely that a substantial amount (at least  $> 50\%$ , see Figure 1) will contribute to air-sea exchange. It also underscores the importance of further studies on constraining rate coefficients and improving our understanding and capability to model microbial oxidation and atmospheric exchange rate coefficients.

#### 2.4.2 What to do?

In my opinion it is by no means strictly necessary to do an assessment like the one iterated above to ensure the necessary scientific quality of the reviewed paper. I let this evaluation be up to the authors and/or editor. The fact that this comment is not peer reviewed and that I am one of the peer reviewers might also make it a bit awkward to include/refer to (I also of course welcome input on my assessment). However, **it is important that the paper appropriately points out that** i) the fate of the laterally advected dissolved methane is very uncertain and difficult to constrain and ii) studies have shown that a considerable amount of dissolved methane contributes to the atmospheric methane budget, even when the methane is released at depth, and iii) the dissolved methane in the laterally advected water masses in the present study is particularly prone to being released to the atmosphere since the methane is injected directly into surface water. This aspect is especially important to focus on if studies like this is used to evaluate the efficacy of using seagrass meadows as biological carbon storages.

## 2.5 Disclaimer

I want to clarify that I am one of the authors of Dølven et al., (2025). It is therefore very convenient of me to refer to the review of MOx rate coefficient values presented therein. There might be more MOx focussed

papers that are more appropriate. I let it be up to the authors and editor to consider whether a reference to that manuscript is appropriate or if it is more appropriate to seek and use references given therein or elsewhere to obtain values for rate coefficients if oxidation rate coefficients will be discussed.

### 3 Smaller line-by-line comments

Line 24-25: Check my comment on dissolved atmospheric flux. This sentence should also be slightly modified.

Line 61 or Line 69: New paragraph. In general, split the text blocks more.

Line 131: Does the insertion of the chambers affect the methane flux to the overlying water? If there's a chance for this, it should be commented on.

Line 145: Is DO (dissolved oxygen) defined?

Line 155: Probably not – horizontally advected, surface water comes from somewhere else.

Line 163: Weird  $\mu$  sign

Line 164: Likely or not? You do the calculation, so you can determine this

Line 165: New paragraph

Line 176-181: What does the range mean? Standard deviation? Not obvious, since the distribution is not Gaussian.

Line 191: Ref my comment on Line 131

Line 242: Higher methane fluxes in sandy areas? Is this correct? This is a bit confusing and the text should clarify expectations and results for sandy vs meadow environments better. Is the sandy area a "control" area? It does not seem like this since the flux seems to be periodically larger there.

Line 252: It is unclear what is meant by "At this concentration, only 0.39 mol CH<sub>4</sub> was present in the water column at any given time." What water column?

## References

- Dølven, K. O., Espenes, H., Hanssen, A., Sert, M. F., Drivdal, M., Randelhoff, A., and Ferré, B. (2025). Modeling water column gas transformation, migration and atmospheric flux from seafloor seepage. *Ocean Science*, 21(6):3031–3054.
- Griffiths, R. P., Caldwell, B. A., Cline, J. D., Broich, W. A., and Morita, R. Y. (1982). Field observations of methane concentrations and oxidation rates in the southeastern bering sea. *Applied and Environmental Microbiology*, 44(2):435–446.
- Gründger, F., Probandt, D., Knittel, K., Carrier, V., Kalenitchenko, D., Silyakova, A., Serov, P., Ferré, B., Svenning, M. M., and Niemann, H. (2021). Seasonal shifts of microbial methane oxidation in arctic shelf waters above gas seeps. *Limnology and Oceanography*, 66(5):1896–1914.
- Jansson, P., Ferré, B., Silyakova, A., Dølven, K., and Omstedt, A. (2019). A new numerical model for understanding free and dissolved gas progression toward the atmosphere in aquatic methane seepage systems. *Limnology and Oceanography: Methods*, 17(3).
- Kessler, J. D., Valentine, D. L., Redmond, M. C., Du, M., Chan, E. W., Mendes, S. D., Quiroz, E. W., Villanueva, C. J., Shusta, S. S., Werra, L. M., Yvon-Lewis, S. A., and Weber, T. C. (2011). A persistent oxygen anomaly reveals the fate of spilled methane in the deep gulf of mexico. *Science*, 331(6015):312–315.
- Leonte, M., Kessler, J. D., Kellermann, M. Y., Arrington, E. C., Valentine, D. L., and Sylva, S. P. (2017). Rapid rates of aerobic methane oxidation at the feather edge of gas hydrate stability in the waters of hudson canyon, us atlantic margin. *Geochimica et Cosmochimica Acta*, 204:375–387.

McGinnis, D. F., Greinert, J., Artemov, Y., Beaubien, S. E., and Wüest, A. (2006). Fate of rising methane bubbles in stratified waters: How much methane reaches the atmosphere? Journal of Geophysical Research: Oceans, 111(C9).

Wanninkhof, R. (2014). Relationship between wind speed and gas exchange over the ocean revisited. Limnology and Oceanography: Methods, 12(JUN):351–362.