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

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Abstract. Seagrass meadows are important blue carbon ecosystems that sequester large amounts of organic carbon but can also emit methane (CH_4), potentially offsetting part of their climate mitigation benefits. However, the seasonal and diurnal dynamics of CH_4 production and emissions in tropical seagrass ecosystems remain poorly understood. This study presents the first integrated assessment of CH_4 cycling in the Haikou seagrass meadow, southern Taiwan. Field campaigns conducted between May 2022 and June 2023 combined surface water sampling, in situ benthic chamber incubations, and porewater profiling in a *Thalassia hemprichii–Halophila pinifolia* seagrass meadow to quantify CH_4 dynamics at both the sediment-to-water and sea-to-air interfaces. The seagrass meadow exhibited higher dissolved CH_4 concentrations and sea-to-air CH_4 fluxes than adjacent coastal waters, confirming that it functions as a localized atmospheric CH_4 hotspot. Nighttime dissolved CH_4 concentrations generally exceeded daytime values, reflecting diurnal variations in oxygen availability, whereas seasonal variability in sea-to-air CH_4 fluxes was primarily driven by wind speed. Mean sediment-to-water and sea-to-air CH_4 fluxes were 88.2 ± 41.2 and 4.9 ± 2.2 μmol m^{-2} d^{-1}, respectively. Despite substantial benthic CH_4 production, atmospheric emissions remained comparatively low, indicating a marked decoupling between sediment-to-water and sea-to-air CH_4 fluxes. This decoupling suggests that much of the sediment-derived CH_4 was transported laterally by tidal exchange and coastal circulation before atmospheric release, with microbial oxidation acting as an additional sink. Compared with adjacent bare sand sediments, seagrass sediments maintained higher baseline CH_4 production rates and benthic fluxes owing to greater organic matter availability and favorable microbial conditions, whereas unvegetated sandy sediments generally exhibited low CH_4 production but produced episodic CH_4 pulses following storm-induced sediment disturbance. Elevated porewater CH_4 concentrations during summer and autumn further indicated enhanced methanogenesis associated with organic matter accumulation under calmer hydrodynamic conditions. Overall, these findings demonstrate that CH_4 cycling in tropical seagrass meadows is jointly regulated by biological processes and hydrodynamic conditions, highlighting the need to consider both CH_4 emissions and carbon sequestration when evaluating the climate benefits of blue carbon ecosystems.

1. Introduction

Human activities, including fossil fuel combustion, industrial processes, land-use change, and deforestation, have rapidly increased greenhouse gas (GHG) emissions over recent decades, driving global warming and ongoing climate change (IPCC, 2021). Achieving climate neutrality requires not only reducing GHG emissions but also protecting and enhancing natural carbon sinks. Preserving and restoring these sinks is therefore recognized as an effective strategy for climate change mitigation (Howard et al., 2023). Among them, coastal blue carbon ecosystems, including mangroves, seagrasses, and salt marshes, play a critical role by sequestering large amounts of organic carbon in their sediments.

Seagrass meadows are among the most efficient natural carbon sinks in coastal environments because they sequester carbon through photosynthesis and store it in sediments for centuries to millennia (Lovelock and Duarte, 2019; Mcleod et al., 2011; Rosentreter et al., 2021; Yau et al., 2023). In addition to long-term carbon storage, seagrasses influence seawater carbonate chemistry through calcium carbonate formation and dissolution (Natividad et al., 2026) and contribute substantially to coastal carbon cycling by exporting dissolved organic carbon and functioning as net trophic habitats (Chen et al., 2026; Chen et al., 2024). Together, these processes enhance the climate mitigation potential of seagrass ecosystems.

Despite these benefits, seagrass meadows are also recognized as sources of methane (CH_4), a potent GHG with a sustained-flux global warming potential 96 times greater than carbon dioxide (CO_2) over a 20-year time horizon on a mass basis (Neubauer and Megonigal, 2015). Depending on seagrass species, geographic setting, and environmental conditions, CH_4 emissions may offset up to 33.4% of the blue carbon sequestered in sediments (Rosentreter et al., 2021; Yau et al., 2023; Eyre et al., 2023). More broadly, the coastal ocean represents a major hotspot of marine CH_4 emissions, with continental shelf sediments estimated to release 18–48 Tg CH_4 yr^{-1} through ebullition alone (Weber et al., 2019).

In coastal waters, CH_4 is primarily produced in sediments through the anaerobic microbial degradation of organic carbon via methanogenesis (Arndt et al., 2013). Although sulfate reduction generally suppresses methanogenesis in marine sediments, both processes can coexist because methanogens utilize non-competitive substrates, such as methylamines and methanol, that are not consumed by sulfate-reducing bacteria (Lyimo et al., 2018; Reeburgh, 2007). CH_4 production within sediments can subsequently be transported to the overlying water column by diffusion, advective exchange, or ebullition and may ultimately be emitted to the atmosphere (Saunois et al., 2020). Although aerobic CH_4 production has also been reported in seagrass meadows, it is generally considered a minor pathway (Schorn et al., 2022).

The magnitude of CH_4 emissions from seagrass meadows varies considerably among regions and habitats because methanogenesis is regulated by organic matter availability, microbial community composition, sediment characteristics, hydrodynamic conditions, and plant-mediated processes (Saunois et al., 2020; Schorn et al., 2022; Sogin et al., 2022; Arndt et al., 2013; Oreska et al., 2020). Consequently, although seagrass meadows generally emit less CH_4 than mangroves and salt marshes (Yau et al., 2023), their net climate benefit remains uncertain and depends on the balance between carbon sequestration and GHG emissions. Quantifying CH_4 production, transport, and emission is therefore essential for accurately evaluating the climate mitigation potential of seagrass ecosystems and for incorporating blue carbon habitats into carbon accounting

frameworks, voluntary carbon markets, and international climate strategies such as the Paris Agreement (Kuwae et al., 2022; Howard et al., 2023).

Despite growing recognition of seagrass-associated CH_4 emissions, studies of CH_4 cycling in tropical seagrass ecosystems remain scarce. This study provides the first comprehensive assessment of CH_4 dynamics in the Haikou seagrass meadow, southern Taiwan. Through three intensive field campaigns combining surface water sampling, in situ benthic chamber incubations, and porewater profiling, we quantified CH_4 fluxes in both seagrass and adjacent bare sandy sediments across the sediment-to-water and sea-to-air interfaces. This integrated approach provides new insights into the temporal variability and environmental controls of CH_4 cycling in tropical seagrass ecosystems and improves our understanding of their role in coastal carbon cycling and climate regulation.

2. Materials and Methods

2.1 Study area and sampling periods

The study site is located at Haikou, Checheng Township, Pingtung County, southern Taiwan (22°5′21.830″N, 120°42′42.408″E; Figure 1). Haikou has a tropical climate. According to observations from the Checheng Weather Station (120.7162°E, 22.0744°N; Figure 1c), mean monthly air temperatures during 2022–2023 ranged from 21.0 to 29.2 °C, monthly total precipitation ranged from 0.5 to 318.8 mm, and mean monthly wind speeds ranged from 1.5 to 5.9 m s^{-1} (Figure 2). The study was conducted in a natural subtidal seagrass meadow covering approximately 4.38 ha and dominated by *Thalassia hemprichii* and *Halophila pinifolia*. According to the seagrass survey reported by Lin et al. (2023), the meadow had a mean seagrass cover of approximately 66%, with seasonal estimates ranging from approximately 45% to 90%. Water depth at the seagrass and bare sand sites varied with the tidal cycle, ranging from approximately 0.5 m at low tide to 1.5 m at high tide. Figure 3 presents a conceptual diagram of the study area, in which the seagrass meadow is bordered seaward by a reef platform, beyond which the water depth increases sharply to approximately 10 m, forming the adjacent offshore coastal waters, hereafter referred to as the coastal water site.

Field investigations were conducted from May 19 to 23 (spring) and September 26 to October 4 (autumn) in 2022, and from June 13 to 17 (summer) in 2023. Winter fieldwork could not be conducted because of severe weather conditions. Surface water samples were collected at both the coastal water site and within the Haikou seagrass meadow during both daytime and nighttime across different seasons to examine the diurnal and seasonal variability of sea-to-air CH_4 fluxes. In situ benthic chamber incubations were conducted simultaneously in the Haikou seagrass meadow and adjacent unvegetated bare sand areas during both daytime and nighttime to investigate the diurnal and seasonal variability of sediment-to-water CH_4 fluxes under changing environmental conditions. Both incubation sites were located in the subtidal zone and experienced similar tidal depth variations. During each field campaign, porewater samples were also collected from the seagrass meadow and adjacent unvegetated bare sand sediments.

2.2 In situ chamber incubation system

In situ benthic incubation experiments were conducted at four sites, including two seagrass meadow sites and two bare sand sites (Figure 1b), to quantify changes in seawater chemical parameters influenced by sediments and benthic organisms in areas with and without seagrass. The closed chambers prevented interference from water exchange and water-air interactions. Designed to preserve the natural structure of aquatic plants and sediment surfaces, the chambers also ensured proper fluid dynamics without altering flow patterns when the lid was closed (Webb and Eyre, 2004). Each benthic chamber measured 40 cm in height and 32 cm in diameter (Figure 4c). Its transparent structure allowed sunlight to penetrate, ensuring that the organisms and plants inside were not affected by shading. Before incubation, all chambers were left open for at least two hours to facilitate water exchange.

The in situ benthic incubation experiments were conducted during both day and night, with incubation durations adjusted according to seasonal weather and sea conditions. In spring, nighttime incubations were conducted for 5 hours, whereas daytime incubations were limited to 3 hours due to unfavorable conditions during the rainy season. In summer, both daytime and nighttime incubations were conducted for 5 hours. In autumn, unstable storm conditions restricted the incubation period to 2 hours. A magnetic agitator was placed inside each chamber to maintain continuous water circulation during incubation (Figure 4d).

2.3 Samples collection and chemical analysis

Incubation water was collected through a three-way valve installed on each chamber at the beginning and end of each incubation for benthic flux calculations. Ambient surface seawater surrounding the incubation setups in the seagrass bed was collected seven times a day at 06:00, 09:00, 12:00, 15:00, 18:00, 21:00, and 24:00. Surface seawater samples were also collected from the coastal water site outside the reef platform at the same times, except at 21:00 and 24:00 due to safety concerns.

Surface and chamber water samples for CH_4 analysis were collected in duplicate using 120 mL brown serum bottles. Bottles were rinsed twice with sample water, filled to slight overflow, and preserved with 200 μL of saturated mercuric chloride ($HgCl_2$) to inhibit microbial activity. After sealing with a butyl rubber stopper and aluminum cap, the bottles were shaken to mix, placed in an ice-filled cooler, transported to the laboratory, and stored at 4 °C in the dark.

Porewater samples were collected using porewater wells and a Luer-Lok syringe at sediment depths of 0, 2, 4, 6, 8, 12, 16, and 20 cm following the method of Falter and Sansone (2000). Samples were immediately transferred into 30 mL brown serum bottles, preserved with 50 μL $HgCl_2$, sealed with butyl rubber stoppers and aluminum caps, placed on ice in a dark cooler during transport, and stored at 4 °C in dark until analysis. Porewater samples were collected from both the seagrass meadow and bare sand sediments at locations separate from the chamber incubation sites to avoid disturbing the ongoing benthic chamber incubations. All seawater and porewater samples were analyzed within two months of collection.

At each water-sampling, water temperature, salinity, and dissolved oxygen (DO) were measured on-site using a portable multiparameter water quality meter (YSI ProDSS, USA), concurrently with the collection of discrete water samples for CH_4 analysis. Dissolved CH_4 concentrations were determined in the laboratory using the headspace technique (Weiss, 1981) and analyzed with a gas chromatograph (GC; Agilent 7890, USA) equipped with a flame ionization detector (FID). Detailed information on column configurations and calibration procedures can be found in Tseng et al. (2022).

2.4 The CH_4 sea-to-air fluxes

CH_4 fluxes at the sea–air interface was calculated using the equation:

$$F_{sea\text{-}air}=k \times (C_{obs}-C_{eq}) \quad (1)$$

where C_{obs} represents the observed concentration of dissolved CH_4 in seawater, C_{eq} denotes the expected equilibrium concentration and k is the gas exchange coefficient. The equilibrium CH_4 concentration was estimated using the solubility equation of Wiesenburg and Guinasso (1979), incorporating in-situ temperature, salinity, and atmospheric CH_4 molar fractions. Atmospheric CH_4 data for May, September, and October 2022, along with June 2023, were sourced from the NOAA Global Monitoring Laboratory (Lan et al., 2026).

The gas exchange coefficient was determined following Wanninkhof (2014):

$$k=0.251 \times u^2 \times \left(\frac{Sc}{660}\right)^{-0.5} \quad (3)$$

Here, Sc is the Schmidt number for CH_4, and u represents wind speed (m/s). Monthly wind speed data were obtained from the Checheng Weather Station (120.7162°E, 22.0744°N), operated by Taiwan's Central Weather Administration.

2.5 The benthic CH_4 production rates and sediment-to-water fluxes

Benthic CH_4 production rates and sediment-to-water fluxes were measured with chambers inserted 10–15 cm into the sediment (Roth et al., 2019). Seawater samples from the chambers were taken at 2 to 5 hours depending on seasonal weather and sea conditions, as described in Section 2.2. Benthic CH_4 production rates and sediment-to-water fluxes were calculated from the change in CH_4 concentration in the overlying chamber water during the incubation period using the following equations:

$$Production\ rate = \left(\frac{\Delta C}{\Delta t}\right) \quad (4)$$

$$F_{sediment\text{-}water} = \left(\frac{\Delta C}{\Delta t}\right) \times \left(\frac{V_{chamber}}{A_{chamber}}\right) \quad (5)$$

where $F_{sediment\text{-}water}$ is sediment-to-water flux (μmol m^{-2} h^{-1} or μmol m^{-2} d^{-1}); ΔC represent the differences in CH_4 concentration (nmol L^{-1}), during the incubation period Δt (hours); $V_{chamber}$ is the volume of overlying water in the chamber (m^3); $A_{chamber}$ is the area of the chamber (m^2). Here, benthic CH_4 production rate refers to the net accumulation rate of CH_4 concentration in the overlying chamber water during incubation and does not represent gross CH_4 production within the sediment.

3. Results

3.1 Seasonal and diurnal variability in surface water conditions

Surface water temperatures ranged from 24.6 to 32.0 ℃. Daytime and nighttime mean temperatures ranged from 28.3–30.0 ℃ and 26.1–28.5 ℃, respectively, in the seagrass meadow, and from 28.7–29.6 ℃ and 26.3–29.2 ℃, respectively, in the coastal water. Seasonal mean temperatures ranged from 27.2 to 29.1 ℃ in the seagrass meadow and from 27.5 to 29.4 ℃ in the coastal water (Table 1). Daytime surface water temperatures were higher than nighttime temperatures (Figure 5a). Salinity ranged from 30.21 to 33.73, with seasonal mean values slightly lower in the seagrass meadow (31.94–32.88) than in the adjacent coastal waters (32.12–33.06; Figure 5b). This difference may reflect the influence of rainfall, with average monthly precipitation ranging from 156 to 261 mm during the study period (Figure 2). DO saturation in the seagrass meadow exhibited pronounced diurnal variation (Figure 5c), increasing from nighttime averages of 87.0–94.5% to daytime averages of 109.3–124.4% (Table 1), likely driven by seagrass photosynthesis. In contrast, DO saturation in the coastal water was relatively stable, ranging from nighttime averages of 97.0–99.3% to daytime averages of 100.5–107.5% (Table 1). Seasonal mean DO saturation ranged from 98.9 to 109.4% in the seagrass meadow, slightly higher than that in the coastal water (99.9–102.8%; Table 1).

3.2 Seasonal and diurnal variability in surface CH_4 concentrations and sea-to-air fluxes

Mean surface CH_4 concentrations were higher in the seagrass meadow than in the adjacent coastal water (Figure 5d). Concentrations in the seagrass meadow ranged from 6.6 to 8.3 nM during the daytime and from 6.9 to 13.1 nM at night, whereas those in the coastal water ranged from 5.4 to 7.4 nM and from 4.2 to 5.4 nM, respectively. Seasonal mean CH_4 concentrations were also higher in the seagrass meadow (7.6–9.9 nM) than in the coastal water (4.9–6.0 nM; Table 1). Sea-to-air CH_4 fluxes exhibited distinct spatial and seasonal patterns, influenced by both surface CH_4 concentrations and wind speed. Monthly mean wind speeds recorded at the Checheng Weather Station were 3.2 m s^{-1} in spring 2022, 2.2 m s^{-1} in summer 2023 and 2.6–5.4 m s^{-1} in autumn 2022 (Table 1). Correspondingly, CH_4 sea-to-air fluxes were higher in the seagrass meadow than in the coastal water across all seasons and times of day (Figure 6a and Figure 7a). In both habitats, the highest sea-to-air CH_4 fluxes occurred in autumn 2022, averaging 6.8 ± 3.1 μmol m^{-2} d^{-1} in the seagrass meadow and 4.9 ± 5.2 μmol m^{-2} d^{-1} in the coastal water (Figure 7a). In spring 2022, mean CH_4 fluxes decreased to 5.4 ± 3.0 μmol m^{-2} d^{-1} in the seagrass meadow and 2.3 ± 0.1 μmol m^{-2} d^{-1} in the coastal water (Figure 7a). The lowest fluxes were observed in summer 2023, averaging 2.5 ± 0.8 μmol m^{-2} d^{-1} in the seagrass meadow and 0.9 ± 0.3 μmol m^{-2} d^{-1} in the coastal water (Figure 7a). This seasonal pattern was consistent with the observed variation in wind speed (Table 1).

3.3 Seasonal and diurnal variability in benthic CH_4 dynamics and sediment-to-water fluxes

For the sediment-to-water CH_4 flux measurements, incubations were conducted at four sites, including two seagrass sites and two adjacent unvegetated bare sand sites. Incubation chambers were deployed at each site, and duplicate water samples were

collected from each chamber at the beginning and end of each incubation for CH_4 analysis. Across the incubation experiments conducted in spring, summer, and autumn, a total of 284 water samples were collected and used to calculate sediment-to-water CH_4 fluxes.

CH_4 benthic fluxes were slightly higher at night than during the day in the seagrass meadow during spring and summer (Figure 6b). Nighttime sediment incubations were not performed during autumn 2022 because storm event prevented field measurements. In the seagrass meadow, CH_4 production rates and sediment-to-water fluxes were 102.9 ± 20.2 μmol m^{-3} d^{-1} and 41.2 ± 8.2 μmol m^{-2} d^{-1} in spring, 295.0 ± 35.1 μmol m^{-3} d^{-1} and 118.0 ± 14.0 μmol m^{-2} d^{-1} in summer, and 263.3 ± 710.4 μmol m^{-3} d^{-1} and 105.3 ± 284.2 μmol m^{-2} d^{-1} in autumn, respectively (Table 2). Overall, CH_4 production rates and sediment-to-water fluxes in the seagrass meadow remained relatively consistent seasonal patterns, although greater variability was observed in autumn (Figure 7b). In contrast, bare sand sediments maintained relatively low CH_4 production rates and sediment-to-water fluxes during spring and summer but exhibited a marked increase in autumn (Figure 7b). In spring, the CH_4 production rate was 42.1 ± 11.1 μmol m^{-3} d^{-1}, with a sediment-to-water flux of 16.9 ± 4.5 μmol m^{-2} d^{-1}. In summer, the CH_4 production rate was 114.0 ± 30.6 μmol m^{-3} d^{-1}, with a sediment-to-water flux of 45.6 ± 12.2 μmol m^{-2} d^{-1}. In autumn, the CH_4 production rate was substantially higher, reaching 972.2 ± 957.1 μmol m^{-3} d^{-1}, accompanied by a sediment-to-water flux of 388.9 ± 382.8 μmol m^{-2} d^{-1} (Table 2).

3.4 Seasonal porewater CH_4 profiles

Porewater CH_4 concentrations ranged from 9.3–282.0 nM in spring 2022, 6.1–256.0 nM in summer 2023, and 9.1–190.3 nM in autumn 2022 in sandy sediments. In seagrass sediments, mean porewater CH_4 concentrations ranged from 8.1–92.0 nM in spring 2022, 11.8–364.8 nM in summer 2023 and 6.7–262.1 nM in autumn 2022 (Figure 8). These patterns broadly corresponding to the observed benthic CH_4 production rates and sediment-to-water fluxes (Table 2). In seagrass sediments, porewater CH_4 concentrations varied with depth, with mean concentrations generally highest within the upper 0–12 cm across all sampling campaigns, before declining below 12 cm depth. Seasonal differences were also evident, with the highest porewater CH_4 concentration recorded during autumn 2022 (423.2 nM), followed by summer 2023 (364.8 nM), whereas spring 2022 exhibited comparatively lower concentrations throughout most of the sediment profile (Figure 8). Seagrass sediments exhibited higher porewater CH_4 concentrations than bare sand sediments in summer 2023 and autumn 2022, particularly within the upper 12 cm of the sediment column (Figure 8b and 8c). However, this pattern was reversed in spring 2022, when bare sand sediments exhibited higher porewater CH_4 concentrations than seagrass sediments below 10 cm depth (Figure 8a). In bare sand sediments, porewater CH_4 concentrations also varied with depth, although vertical gradients were less consistent among seasons than those observed in seagrass sediments. Concentrations generally remained within a narrower range across the sediment profile (Figure 8).

4. Discussion

4.1 Controls on dissolved CH_4 dynamics and sea-to-air fluxes in a tropical seagrass meadow

Dissolved CH_4 concentrations in the seagrass meadow exhibited diurnal variability, with surface waters peaking at night in spring 2022 and summer 2023 (Figure 5d). This pattern likely reflects the influence of daytime photosynthesis, which increased DO saturation and may have suppressed CH_4 production or enhanced aerobic CH_4 oxidation, thereby limiting CH_4 accumulation in the water column. In contrast, lower nighttime DO saturation reduced oxidation potential and allowed sediment-derived CH_4 to accumulate in the shallow water column. However, the exception occurred during autumn 2022, when the typical diurnal pattern was disrupted by a nighttime storm event characterized by heavy rainfall and strong winds. Elevated wind speeds likely enhanced turbulence, vertical mixing, and air–water gas exchange, promoting rapid physical degassing of dissolved CH_4 and resulting in substantially lower nighttime concentrations than those observed during the other sampling periods. This finding highlights the importance of episodic weather events in regulating short-term CH_4 dynamics in shallow coastal ecosystems.

Compared with the seagrass meadow, the adjacent coastal waters exhibited lower and less variable dissolved CH_4 concentrations in the surface water. This contrast is likely attributable to the substantially greater water depth (approximately 10 m) at the adjacent coastal water site, which reduces the influence of sediment-derived CH_4 on surface waters. In contrast, the shallow water depth (0.5–1.5 m) within the seagrass meadow facilitates the transport of benthic CH_4 to the surface, resulting in higher dissolved CH_4 concentrations in the surface water. Although no significant seasonal differences in surface CH_4 concentrations were observed in either sampling sites, both the seagrass meadow and adjacent coastal waters acted as net sources of atmospheric CH_4 throughout the study period. Mean sea-to-air CH_4 fluxes were higher in the seagrass meadow (4.9 ± 2.2 μmol m^{-2} d^{-1}) than in the adjacent coastal waters (2.7 ± 2.0 μmol m^{-2} d^{-1}; Table 1), indicating that seagrass habitats function as localized CH_4 emission hotspots. These estimates, however, should be interpreted as seasonal baseline fluxes rather than annual budgets because winter sampling could not be conducted due to severe weather conditions, and the autumn observations were strongly influenced by an extreme storm event. The absence of significant seasonal changes in dissolved CH_4 concentrations further suggests that seasonal variability in sea-to-air CH_4 fluxes was primarily governed by changes in wind speed rather than by variations in dissolved CH_4 concentrations, highlighting the dominant role of physical gas transfer in regulating atmospheric CH_4 emissions. Although seagrass meadows are widely recognized for their capacity to sequester carbon over long timescales (Duarte et al., 2013; Fourqurean et al., 2012; Mcleod et al., 2011), our findings demonstrate that they also function as localized atmospheric CH_4 sources. These results emphasize that evaluations of the climate benefits of seagrass ecosystems should consider both their carbon sequestration capacity and their CH_4 emissions, particularly as changes in hydrodynamic conditions and extreme weather events may alter CH_4 exchange between sediment, water and the atmosphere.

4.2 Drivers of seasonal benthic CH_4 production and sediment-to-water fluxes in a tropical seagrass meadow

CH_4 production and benthic fluxes in the seagrass meadow exhibited seasonal variability, with the lowest rates occurring in spring and substantially higher rates during summer and autumn (Figure 7b). This seasonal pattern is likely driven by changes in hydrodynamic conditions that regulate organic matter accumulation within the meadow. At Haikou, strong winds and wave action prevail from October to April (Figure 2), limiting the deposition and retention of organic particles within the seagrass bed. Consequently, the availability of organic substrates for methanogenesis is reduced, resulting in relatively low benthic CH_4 production and sediment-to-water fluxes during spring. In contrast, calmer conditions beginning in late spring and early summer favor the deposition and accumulation of organic matter, including seagrass detritus and epiphytic material, within the sediment. The enhanced availability of labile organic carbon likely stimulates microbial decomposition and methanogenesis, leading to the elevated benthic CH_4 production rates and sediment-to-water fluxes observed during summer and autumn.

The seasonal increase in benthic CH_4 production is supported by the porewater CH_4 profiles, which showed higher concentrations during summer and autumn (Figure 8). According to Tang et al. (2025), sediments in the Haikou seagrass meadow contain an average total organic carbon content of approximately 0.40%, with organic matter derived predominantly from marine sources, including aquatic plant material and microbial processing. The accumulation of this organic substrate provides the fuel required for microbial methanogenesis and likely explains the elevated porewater CH_4 concentrations observed during the warmer seasons.

Porewater CH_4 concentrations were consistently higher than those in the overlying water, indicating that sediment diffusion represented the primary pathway supplying CH_4 to the water column (Yu et al., 2024). However, only a fraction of the CH_4 produced in sediments is ultimately emitted to the atmosphere because substantial oxidation can occur before reaching the water surface. In addition, the decline in porewater CH_4 concentrations with sediment depth observed in this study is consistent with previous findings that sulfate-dependent anaerobic oxidation of CH_4 and competition for electron acceptors can limit CH_4 accumulation in deeper anoxic sediments (Rissanen et al., 2017). Although diffusion was the dominant transport pathway quantified in this study, ebullition may also contribute to CH_4 release when porewater CH_4 partial pressure exceeds hydrostatic pressure, allowing CH_4 bubbles to bypass oxidation within the sediment and water column (Sun et al., 2022). Therefore, the observed porewater CH_4 distributions likely reflect a dynamic balance among organic matter availability, microbial methanogenesis, aerobic and anaerobic CH_4 oxidation, and multiple transport pathways from sediment to the overlying water (Henriksson et al., 2024; Yau et al., 2023).

Overall, these findings indicate that seasonal hydrodynamic conditions indirectly regulate CH_4 emissions from the seagrass meadow by controlling the accumulation of organic matter available for methanogenesis. The combination of enhanced organic carbon deposition during calm periods, active microbial CH_4 production, and sediment-to-water transport explains the elevated sediment-to-water CH_4 fluxes observed during summer and autumn, while subsequent oxidation within the sediment and water column moderates the fraction of CH_4 ultimately released to the atmosphere.

4.3 Contrasting benthic CH_4 dynamics between seagrass and sandy sediments

In situ benthic chamber incubations demonstrated differences in CH_4 dynamics between seagrass and adjacent bare sand sediments. During both daytime and nighttime in spring 2022 and summer 2023, benthic CH_4 production rates and sediment-to-water fluxes were higher in seagrass sediments than in adjacent bare sand sediments (Figure 6b and 7b). These differences reflect fundamental ecological and microbial contrasts between vegetated and unvegetated habitats. Seagrass meadows are highly productive ecosystems that contribute substantial quantities of organic matter to the sediments, providing abundant substrates for microbial decomposition and methanogenesis (Yau et al., 2023). In addition, seagrass roots modify sediment biogeochemistry by regulating oxygen availability and shaping microbial community composition, thereby influencing the balance between methanogenic archaea and methanotrophic bacteria (George et al., 2020). Liang et al. (2025) further demonstrated that seagrass sediments harbor a higher abundance of methanogenic archaea than adjacent unvegetated sediments, providing a microbial basis for the elevated CH_4 production observed in this study. Reduced oxygen penetration within the rhizosphere, together with active microbial communities, further promotes methanogenesis (Henriksson et al., 2024). Moreover, seagrass plants possess specialized gas-conducting tissues (aerenchyma) that facilitate internal gas transport. While these tissues primarily transport oxygen to belowground tissues, they can also provide pathways for sediment-derived CH_4 to diffuse or escape into the overlying water column, thereby enhancing CH_4 emissions from seagrass habitats (Yau et al., 2023; Li et al., 2021). Collectively, these biological and biogeochemical processes explain why seagrass sediments generally support higher CH_4 production and more sustained sediment-to-water fluxes than adjacent bare sand sediments (George et al., 2020; Schorn et al., 2022).

An exception to this general pattern occurred during the autumn 2022 sampling, when daytime benthic CH_4 production rates and sediment-to-water fluxes in bare sand sediments exceeded those in the seagrass meadow, while nighttime incubations could not be conducted because of the storm event (Figure 6b). This anomaly was likely caused by heavy rainfall and strong winds that disturbed the unvegetated sandy sediments, promoting sediment resuspension and the rapid release of porewater CH_4. In contrast, the dense root and rhizome network of seagrasses stabilizes sediments and buffers against physical disturbance, making vegetated sediments less susceptible to storm-induced CH_4 pulses despite their generally higher background CH_4 production.

These contrasting responses were also reflected in the seasonal averages. Mean sediment-to-water CH_4 fluxes were 88.2 ± 41.2 μmol m^{-2} d^{-1} in the seagrass meadow and 150.4 ± 207.0 μmol m^{-2} d^{-1} in the adjacent bare sand sediments (Table 2). However, the higher seasonal mean for bare sand sediments was largely driven by the exceptionally high emissions recorded during the storm-affected autumn sampling. Excluding this episodic event, seagrass sediments exhibited higher baseline CH_4 production and sediment-to-water fluxes, whereas bare sand sediments generally maintained much lower emissions. These findings indicate that seagrass sediments function as persistent CH_4 sources sustained by continuous organic matter decomposition and microbial methanogenesis, whereas unvegetated bare sand sediments are characterized by relatively low background emissions punctuated by irregular, disturbance-driven CH_4 pulses. As climate change is projected to increase the intensity and frequency

of typhoons and other extreme weather events (IPCC, 2021), episodic CH_4 release from unvegetated coastal sediments may become an increasingly important component of coastal GHG budgets, even though seagrass meadows remain the dominant long-term hotspots for benthic CH_4 production.

4.4 The fate of sediment-derived CH_4 in a tropical seagrass meadow

Despite acting as a net atmospheric CH_4 source, sediment-to-water CH_4 fluxes in the seagrass meadow were one to two orders of magnitude greater than the corresponding sea-to-air fluxes, indicating a substantial decoupling between benthic CH_4 production and atmospheric emissions. A simple mass-balance comparison further demonstrates that only a small fraction of sediment-derived CH_4 ultimately escaped to the atmosphere. Based on the estimated meadow area (4.38 ha) and an average water depth of 1 m, sediments released approximately 162, 465, and 415 mole CH_4 into the overlying water column during spring, summer, and autumn, respectively. In comparison, only 21, 10, and 27 mole CH_4 were emitted to the atmosphere during the corresponding sampling periods. Consequently, approximately 87% of sediment-derived CH_4 in spring, 98% in summer, and 94% in autumn did not reach the atmosphere directly. Instead, much of this CH_4 was likely transported laterally by tidal exchange and coastal circulation, while a smaller fraction was consumed through microbial oxidation within the sediment and water column before atmospheric release. The relatively small standing stock of dissolved CH_4 in the water column (0.33–0.43 mole across seasons), despite substantial benthic inputs, further supports the rapid turnover and efficient redistribution of CH_4 within this shallow, hydrodynamically active seagrass ecosystem.

These findings demonstrate that benthic CH_4 production cannot be directly translated into atmospheric emissions. Rather, the fate of sediment-derived CH_4 is primarily governed by lateral transport driven by tidal exchange and coastal circulation, together with microbial oxidation and physical gas exchange, all of which regulate the fraction ultimately released to the atmosphere. However, this interpretation should be considered in light of several methodological limitations. Although in situ benthic chamber incubations are among the most representative approaches for quantifying sediment-to-water fluxes because they preserve the natural sediment-water interface while maintaining ambient light conditions, hydrodynamics, and biological interactions (Mallon et al., 2022), the chamber environment may still influence measured fluxes. Over the incubation period, changes in oxygen availability and microbial activity can alter CH_4 production and oxidation rates, particularly during longer deployments (Villnas et al., 2012). In addition, environmental conditions within the chamber may become more stable than in the surrounding environment, potentially enhancing photosynthetic activity and metabolic rates (Olivé et al., 2016). Conversely, shading by the chamber and suspended particles may reduce light penetration and photosynthetic efficiency, thereby affecting oxygen production and CH_4 oxidation (Mallon et al., 2022). Although these factors are unlikely to alter the observed habitat-specific and seasonal patterns, they may influence the absolute magnitude of the measured benthic fluxes.

Furthermore, the relative contributions of lateral transport and microbial oxidation could not be quantified directly in this study. Given the shallow water depth (0.5–1.5 m) and frequent tidal exchange within the Haikou seagrass meadow, lateral transport is likely to represent the dominant pathway for removing sediment-derived CH_4 from the meadow before atmospheric emission. Future studies integrating hydrodynamic observations, direct measurements of CH_4 oxidation rates, and continuous

flux measurements across tidal cycles will help better constrain the fate of sediment-derived CH_4 and improve GHG budgets for blue carbon ecosystems.

4.5 Regional and global context of CH_4 fluxes in seagrass ecosystems

In a broader geographic context, the sea-to-air CH_4 fluxes measured at Haikou were comparable to those reported for seagrass meadows at Koh Mook, Thailand (Halim et al., 2024), and Swan Lake, China (Tan et al., 2025), suggesting similar CH_4 emission characteristics among several Southeast Asian seagrass ecosystems (Table 3). However, the fluxes were substantially lower than those reported from the Chilika Lagoon, India (Banerjee et al., 2018), where tropical seagrass meadows exhibited considerably higher CH_4 emissions that were further enhanced under warming conditions through methylotrophic methanogenesis (Dai et al., 2025). Likewise, studies from the Caribbean have reported elevated CH_4 emissions from organic-rich, anoxic seagrass sediments, although seasonal variability and oxygen transport by seagrass plants can moderate net emissions (Saderne et al., 2023). Globally, seagrass ecosystems are generally recognized as net CH_4 sources, with a mean sea-to-air flux of 79.0 μmol m^{-2} d^{-1} (Eyre et al., 2023), substantially higher than the fluxes observed at Haikou. According to Eyre et al. (2023), the highest CH_4 emissions are typically associated with lagoons and salt marshes, where abundant plant-derived methylated compounds promote methylotrophic methanogenesis.

The sediment-to-water CH_4 fluxes measured in this study also fell within the range reported for other seagrass ecosystems (Table 3). The observed fluxes were comparable to those measured in *Enhalus acoroides* meadows in Awerange Bay, Indonesia (Alongi et al., 2008), exceeded those reported for *Halophila ovalis* and *Zostera muelleri* meadows in Wallis Lake, Australia (Camillini, 2020), but remained lower than fluxes measured in *Posidonia australis* meadows in Wallis Lake (Camillini, 2020) and seagrass habitats in South Bay, Virginia (Oreska et al., 2020). These differences underscore the importance of local environmental conditions, including sediment organic matter content, redox conditions, hydrodynamics, and nutrient availability, in regulating sediment methanogenesis and CH_4 transport. In addition, species-specific traits, such as belowground biomass, root oxygen release, and organic matter inputs, are likely to contribute to differences in sediment-to-water CH_4 fluxes among seagrass meadows (Garcias-Bonet and Duarte, 2017).

Taken together, these findings highlight the importance of region- and species-specific assessments when evaluating the contribution of seagrass ecosystems to GHG budgets. Tropical seagrass meadows differ fundamentally from temperate systems in their biogeochemical characteristics, microbial processes, and exposure to environmental disturbances, all of which influence CH_4 production and emissions (Pajares et al., 2017). Future studies should integrate microbial community analyses, porewater geochemistry, isotopic tracers, and trait-based approaches to better resolve the mechanisms controlling CH_4 cycling across different seagrass ecosystems. Such efforts are particularly important in tropical regions, where CH_4 emissions have the potential to offset a substantial proportion of the climate mitigation benefits associated with blue carbon storage. Although the sea-to-air CH_4 fluxes measured at Haikou were relatively low compared with the global average, the elevated benthic CH_4 production within the seagrass meadow and the potential for episodic, weather-driven CH_4 release underscore the need for habitat-specific assessments that consider both carbon sequestration and GHG emissions. These findings are consistent with

the global synthesis of Eyre et al. (2023), which demonstrated that CH_4 emissions can partially offset the climate mitigation benefits of seagrass ecosystems and therefore should be incorporated into comprehensive blue carbon assessments.

5. Conclusions

This study provides the first integrated assessment of seasonal and diurnal CH_4 dynamics linking benthic CH_4 production, sediment-to-water fluxes, and sea-to-air emissions in a tropical *Thalassia hemprichii* and *Halophila pinifolia* seagrass meadow in Haikou, Taiwan. The seagrass meadow exhibited higher dissolved CH_4 concentrations and sea-to-air CH_4 fluxes than adjacent coastal waters, confirming that it functions as a localized atmospheric CH_4 hotspot. Seasonal variability in atmospheric CH_4 emissions was primarily controlled by wind-driven gas exchange rather than changes in dissolved CH_4 concentrations in the surface water, while benthic CH_4 production and sediment-to-water fluxes were strongly influenced by seasonal hydrodynamic conditions that regulated organic matter accumulation and microbial methanogenesis. Compared with adjacent bare sand sediments, seagrass sediments maintained higher baseline benthic CH_4 production and sediment-to-water fluxes owing to greater organic matter availability and favorable microbial conditions, although storm-induced sediment disturbance generated episodic CH_4 release from unvegetated bare sand sediments.

Despite substantial benthic CH_4 production, only a small proportion of sediment-derived CH_4 was emitted directly to the atmosphere, indicating a pronounced decoupling between sediment production and atmospheric emissions. The majority of CH_4 was likely transported laterally by tidal exchange and coastal circulation before atmospheric release, with microbial oxidation providing an additional sink within the sediment and water column. Although the sea-to-air CH_4 fluxes measured at Haikou were lower than the global average for seagrass ecosystems, the benthic CH_4 fluxes fell within the range reported worldwide, emphasizing the importance of local environmental conditions and species-specific characteristics in regulating CH_4 cycling. These findings demonstrate that evaluating the climate benefits of blue carbon ecosystems requires consideration of both carbon sequestration and GHG emissions. Future studies integrating hydrodynamic measurements, microbial community analyses, CH_4 oxidation rates, and continuous observations across tidal and seasonal cycles will improve our understanding of the fate of sediment-derived CH_4 and reduce uncertainties in blue carbon GHG budgets under future environmental change.

Data availability

Raw data are available on Zenodo (https://doi.org/10.5281/zenodo.19079213, Tseng, 2026).

Author contributions

Hsiao-Chun Tseng: Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. Agnes Sonya Meilani Lumban Gaol: Writing – original draft, Investigation, Formal analysis,

Data curation. Fu-Hsuen Lin: Investigation, Project administration, Data curation. Jian-Jhih Chen: Writing – review and editing, Methodology, Investigation, Conceptualization. Wen-Chen Chou: Writing – review and editing, Methodology, Investigation, Resources, Funding acquisition, Conceptualization.

Competing interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Al-Haj, A. N., Chidsey, T., and Fulweiler, R. W.: Two temperate seagrass meadows are negligible sources of methane and nitrous oxide, Limnology and Oceanography, 67, 10.1002/lno.12250, 2022.

Alongi, D. M., Trott, L. A., Undu, M. C., and Tirendi, F.: Benthic microbial metabolism in seagrass meadows along a carbonate gradient in Sulawesi, Indonesia, Aquatic Microbial Ecology, 51, 141-152, 10.3354/ame01191, 2008.

Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J. J., Pancost, R. D., and Regnier, P.: Quantifying the degradation of organic matter in marine sediments: A review and synthesis, Earth-Science Reviews, 123, 53-86, https://doi.org/10.1016/j.earscirev.2013.02.008, 2013.

Banerjee, K., Paneerselvam, A., Ramachandran, P., Ganguly, D., Singh, G., and Ramesh, R.: Seagrass and macrophyte mediated CO2 and CH4 dynamics in shallow coastal waters, PLoS One, 13, e0203922, 10.1371/journal.pone.0203922, 2018.

Camillini, N.: Carbon and Nitrogen Cycling in Seagrass Ecosystems., PhD thesis, Southern Cross University and University of Southern Denmark, 10.25918/thesis.152, 2020.

Chen, J.-J., Wang, S.-L., Chou, W.-C., Shiu, R.-F., Tseng, H.-C., Chen, T.-Y., and Natividad, M. B.: Habitat-specific metabolism, dissolved organic carbon fluxes, and composition in a tropical seagrass meadow, Estuarine, Coastal and Shelf Science, 336, 10.1016/j.ecss.2026.109864, 2026.

Chen, T.-Y., Chen, J.-J., and Chou, W.-C.: Rethinking blue carbon: unlocking invisible carbon sinks, Environmental Research Letters, 19, 10.1088/1748-9326/ad7044, 2024.

Dai, G., Chen, X., Zhuang, G., Zhang, Y., Zhu, P., Ju, F., and Li, L.: High Methane Production and Emission From Tropical Seagrasses Through Methylotrophic Methanogenesis, Geophysical Research Letters, 52, e2024GL113824, https://doi.org/10.1029/2024GL113824, 2025.

Duarte, C. M., Kennedy, H., Marbà, N., and Hendriks, I.: Assessing the capacity of seagrass meadows for carbon burial: Current limitations and future strategies, Ocean & Coastal Management, 83, 32-38, https://doi.org/10.1016/j.ocecoaman.2011.09.001, 2013.

Eyre, B. D., Camillini, N., Glud, R. N., and Rosentreter, J. A.: The climate benefit of seagrass blue carbon is reduced by methane fluxes and enhanced by nitrous oxide fluxes, Communications Earth & Environment, 4, 10.1038/s43247-023-01022-x, 2023.

Falter, J. L. and Sansone, F. J.: Shallow pore water sampling in reef sediments, Coral Reefs, 19, 93-97, 10.1007/s003380050233, 2000.

Fourqurean, J. W., Duarte, C. M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M. A., Apostolaki, E. T., Kendrick, G. A., Krause-Jensen, D., McGlathery, K. J., and Serrano, O.: Seagrass ecosystems as a globally significant carbon stock, Nature Geoscience, 5, 505-509, 10.1038/ngeo1477, 2012.

Garcias-Bonet, N. and Duarte, C. M.: Methane Production by Seagrass Ecosystems in the Red Sea, Frontiers in Marine Science, 4, 10.3389/fmars.2017.00340, 2017.

George, R., Gullstrom, M., Mtolera, M. S. P., Lyimo, T. J., and Bjork, M.: Methane emission and sulfide levels increase in tropical seagrass sediments during temperature stress: A mesocosm experiment, Ecol Evol, 10, 1917-1928, 10.1002/ece3.6009, 2020.

Halim, M., Stankovic, M., and Prathep, A.: A preliminary study of carbon dioxide and methane emissions from patchy tropical seagrass meadows in Thailand, PeerJ, 12, e18087, 10.7717/peerj.18087, 2024.

Henriksson, L., Yau, Y. Y. Y., Majtényi-Hill, C., Ljungberg, W., Tomer, A. S., Zhao, S., Wang, F., Cabral, A., Asplund, M., and Santos, I. R.: Drivers of Seasonal and Diel Methane Emissions From a Seagrass Ecosystem, Journal of Geophysical Research: Biogeosciences, 129, 10.1029/2024jg008079, 2024.

Howard, J., Sutton-Grier, A. E., Smart, L. S., Lopes, C. C., Hamilton, J., Kleypas, J., Simpson, S., McGowan, J., Pessarrodona, A., Alleway, H. K., and Landis, E.: Blue carbon pathways for climate mitigation: Known, emerging and unlikely, Marine Policy, 156, 10.1016/j.marpol.2023.105788, 2023.

IPCC: Changing State of the Climate System. In Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 287-422, 10.1017/9781009157896.004, 2021.

Kuwae, T., Watanabe, A., Yoshihara, S., Suehiro, F., and Sugimura, Y.: Implementation of blue carbon offset crediting for seagrass meadows, macroalgal beds, and macroalgae farming in Japan, Marine Policy, 138, 10.1016/j.marpol.2022.104996, 2022.

Lan, X., Thoning, K. W., and Dlugokencky, E. J.: Trends in globally-averaged CH4, N2O, and SF6 determined from NOAA Global Monitoring Laboratory measurements. Version 2026-07, https://doi.org/10.15138/P8XG-AA10, 2026.

Li, L., Jiang, Z., Wu, Y., He, J., Fang, Y., Lin, J., Liu, S., and Huang, X.: Interspecific differences in root exudation for three tropical seagrasses and sediment pore-water dissolved organic carbon beneath them, Mar Pollut Bull, 173, 113059, 10.1016/j.marpolbul.2021.113059, 2021.

Liang, T., Dong, J., Zhou, W., Huang, X., Liu, H., Zhang, Y., Yang, Q., Ahmad, M., Chen, L., and Ling, J.: Investigation on the aerobic methanotrophic community and the dominant taxon Methylomarinum in seagrass ecosystem, Environmental Microbiome, 20, 67, 10.1186/s40793-025-00736-z, 2025.

Lovelock, C. E. and Duarte, C. M.: Dimensions of Blue Carbon and emerging perspectives, Biol Lett, 15, 20180781, 10.1098/rsbl.2018.0781, 2019.

Lyimo, L. D., Gullström, M., Lyimo, T. J., Deyanova, D., Dahl, M., Hamisi, M. I., and Björk, M.: Shading and simulated grazing increase the sulphide pool and methane emission in a tropical seagrass meadow, Marine Pollution Bulletin, 134, 89-93, https://doi.org/10.1016/j.marpolbul.2017.09.005, 2018.

Mallon, J., Banaszak, A. T., Donachie, L., Exton, D., Cyronak, T., Balke, T., and Bass, A. M.: A low-cost benthic incubation chamber for in-situ community metabolism measurements, PeerJ, 10, e13116, 10.7717/peerj.13116, 2022.

McLeod, E., Chmura, G. L., Bouillon, S., Salm, R., Björk, M., Duarte, C. M., Lovelock, C. E., Schlesinger, W. H., and Silliman, B. R.: A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO2, Frontiers in Ecology and the Environment, 9, 552-560, 10.1890/110004, 2011.

Natividad, M. B., Cai, W.-J., Bednaršek, N., Chen, J.-J., and Chou, W.-C.: Organic–inorganic carbon coupling shapes carbon dioxide fluxes in seagrass ecosystems, Communications Earth & Environment, 7, 10.1038/s43247-026-03805-4, 2026.

Neubauer, S. C. and Megonigal, J. P.: Moving Beyond Global Warming Potentials to Quantify the Climatic Role of Ecosystems, Ecosystems, 18, 1000-1013, 10.1007/s10021-015-9879-4, 2015.

Olivé, I., Silva, J., Costa, M. M., and Santos, R.: Estimating Seagrass Community Metabolism Using Benthic Chambers: The Effect of Incubation Time, Estuaries and Coasts, 39, 138-144, 10.1007/s12237-015-9973-z, 2016.

Oreska, M. P. J., McGlathery, K. J., Aoki, L. R., Berger, A. C., Berg, P., and Mullins, L.: The greenhouse gas offset potential from seagrass restoration, Sci Rep, 10, 7325, 10.1038/s41598-020-64094-1, 2020.

Pajares, S., Bohannan, B. J. M., and Souza, V.: The Role of Microbial Communities in Tropical Ecosystems, Frontiers in Microbiology, 10.3389/978-2-88945-067-1, 2017.

Reeburgh, W. S.: Oceanic Methane Biogeochemistry, Chemical Reviews, 107 (2), 486-513, 10.1021/cr050362v, 2007.

Rissanen, A. J., Karvinen, A., Nykanen, H., Peura, S., Tiirola, M., Maki, A., and Kankaala, P.: Effects of alternative electron acceptors on the activity and community structure of methane-producing and consuming microbes in the sediments of two shallow boreal lakes, FEMS Microbiol Ecol, 93, 10.1093/femsec/fix078, 2017.

Rosentreter, J. A., Borges, A. V., Deemer, B. R., Holgerson, M. A., Liu, S., Song, C., Melack, J., Raymond, P. A., Duarte, C. M., Allen, G. H., Olefeldt, D., Poulter, B., Battin, T. I., and Eyre, B. D.: Half of global methane emissions come from highly variable aquatic ecosystem sources, Nature Geoscience, 14, 225-230, 10.1038/s41561-021-00715-2, 2021.

Roth, F., Wild, C., Carvalho, S., Rädecker, N., Voolstra, C. R., Kürten, B., Anlauf, H., El-Khaled, Y. C., Carolan, R., Jones, B. H., and Trueman, C.: An in situ approach for measuring biogeochemical fluxes in structurally complex benthic communities, Methods in Ecology and Evolution, 10, 712-725, 10.1111/2041-210x.13151, 2019.

Saderne, V., Dunne, A. F., Rich, W. A., Cadiz, R., Carvalho, S., Cúrdia, J., and Kattan, A.: Seasonality of methane and carbon dioxide emissions in tropical seagrass and unvegetated ecosystems, Communications Earth & Environment, 4, 10.1038/s43247-023-00759-9, 2023.

Saunois, M., Stavert, A. R., Poulter, B., Bousquet, P., Canadell, J. G., Jackson, R. B., Raymond, P. A., Dlugokencky, E. J., Houweling, S., Patra, P. K., Ciais, P., Arora, V. K., Bastviken, D., Bergamaschi, P., Blake, D. R., Brailsford, G., Bruhwiler, L., Carlson, K. M., Carrol, M., Castaldi, S., Chandra, N., Crevoisier, C., Crill, P. M., Covey, K., Curry, C. L., Etiope, G., Frankenberg, C., Gedney, N., Hegglin, M. I., Höglund-Isaksson, L., Hugelius, G., Ishizawa, M., Ito, A., Janssens-Maenhout, G., Jensen, K. M., Joos, F., Kleinen, T., Krummel, P. B., Langenfelds, R. L., Laruelle, G. G., Liu, L., Machida, T., Maksyutov, S., McDonald, K. C., McNorton, J., Miller, P. A., Melton, J. R., Morino, I., Müller, J., Murguia-Flores, F., Naik, V., Niwa, Y., Noce, S., O'Doherty, S., Parker, R. J., Peng, C., Peng, S., Peters, G. P., Prigent, C., Prinn, R., Ramonet, M., Regnier, P., Riley, W. J., Rosentreter, J. A., Segers, A., Simpson, I. J., Shi, H., Smith, S. J., Steele, L. P., Thornton, B. F., Tian, H., Tohjima, Y., Tubiello, F. N., Tsuruta, A., Viovy, N., Voulgarakis, A., Weber, T. S., van Weele, M., van der Werf, G. R., Weiss, R. F., Worthy, D., Wunch, D., Yin, Y., Yoshida, Y., Zhang, W., Zhang, Z., Zhao, Y., Zheng, B., Zhu, Q., Zhu, Q., and Zhuang, Q.: The Global Methane Budget 2000–2017, Earth System Science Data, 12, 1561-1623, 10.5194/essd-12-1561-2020, 2020.

Schorn, S., Ahmerkamp, S., Bullock, E., Weber, M., Lott, C., Liebeke, M., Lavik, G., Kuypers, M. M. M., Graf, J. S., and Milucka, J.: Diverse methylotrophic methanogenic archaea cause high methane emissions from seagrass meadows, Proc Natl Acad Sci U S A, 119, 10.1073/pnas.2106628119, 2022.

Sogin, E. M., Michellod, D., Gruber-Vodicka, H. R., Bourceau, P., Geier, B., Meier, D. V., Seidel, M., Ahmerkamp, S., Schorn, S., D'Angelo, G., Procaccini, G., Dubilier, N., and Liebeke, M.: Sugars dominate the seagrass rhizosphere, Nat Ecol Evol, 10.1038/s41559-022-01740-z, 2022.

Sun, H., Yu, R., Liu, X., Cao, Z., Li, X., Zhang, Z., Wang, J., Zhuang, S., Ge, Z., Zhang, L., Sun, L., Lorke, A., Yang, J., Lu, C., and Lu, X.: Drivers of spatial and seasonal variations of CO2 and CH4 fluxes at the sediment water interface in a shallow eutrophic lake, Water Research, 222, 118916, https://doi.org/10.1016/j.watres.2022.118916, 2022.

Tan, W., Zhong, Z., He, Q., Yun, X., Yang, L., Wang, X., Ji, D., Wang, G., Zhao, J., and Zhang, X.: Methane emission fluxes and associated microbial community characteristics in a temperate seagrass meadow, Science of The Total Environment, 958, 177991, https://doi.org/10.1016/j.scitotenv.2024.177991, 2025.

Tang, Z.-W., Chen, H.-F., Puntu, J. M., Chang, P.-Y., Lo, L., Chen, J.-J., Chou, W.-C., Fan, L.-F., and Chang, Y.-J.: Evaluation of Carbon Sequestration in Seagrass Meadows of Kenting: A Comparative Study with Penghu and Dongsha Island, Journal of Marine Science and Technology, 33, 10.51400/2709-6998.2775, 2025.

Tseng, H.-C., Lin, C.-C., Pan, H.-J., Han, Y. T. Y., and Gong, G.-C.: Seasonal Distributions of Methane in a Populous Urban Coastal Sea Area, Frontiers in Marine Science, 9, 10.3389/fmars.2022.843549, 2022.

Villnas, A., Norkko, J., Lukkari, K., Hewitt, J., and Norkko, A.: Consequences of increasing hypoxic disturbance on benthic communities and ecosystem functioning, PLoS One, 7, e44920, 10.1371/journal.pone.0044920, 2012.

Wanninkhof, R.: Relationship between wind speed and gas exchange over the ocean revisited, Limnology and Oceanography: Methods, 12, 351-362, 10.4319/lom.2014.12.351, 2014.

Webb, A. P. and Eyre, B. D.: Effect of natural populations of burrowing thalassinidean shrimp on sediment irrigation, benthic metabolism, nutrient fluxes and denitrification, Marine Ecology Progress Series, 268, 205-220, 10.3354/meps268205, 2004.

Weber, T., Wiseman, N. A., and Kock, A.: Global ocean methane emissions dominated by shallow coastal waters, Nat Commun, 10, 4584, 10.1038/s41467-019-12541-7, 2019.

Weiss, R. F.: Determinations of Carbon Dioxide and Methane by Dual Catalyst Flame lonization Chromatography and Nitrous Oxide by Electron Capture Chromatography, Journal of Chromatographic Science, 91, 612-616, 10.1093/chromsci/19.12.611, 1981.

Wiesenburg, D. A. and Guinasso, N. L., Jr.: Equilibrium Solubilities of Methane,Carbon Monoxide, and Hydrogen in Water and Sea Water, Journal of Chemical and Engineering Dafa, 24 (4), 356-360, 10.1021/je60083a006, 1979.

Yau, Y. Y. Y., Reithmaier, G., Majtényi-Hill, C., Serrano, O., Piñeiro-Juncal, N., Dahl, M., Mateo, M. A., Bonaglia, S., and Santos, I. R.: Methane Emissions in Seagrass Meadows as a Small Offset to Carbon Sequestration, Journal of Geophysical Research: Biogeosciences, 128, 10.1029/2022jg007295, 2023.

Yu, H., Coffin, R., and Organ, H.: Dynamics of methane emissions from northwestern Gulf of Mexico subtropical seagrass meadows, Biogeochemistry, 167, 723-741, 10.1007/s10533-024-01138-y, 2024.

Table 1. Diurnal and seasonal variations in marine environmental conditions, surface CH_4 concentrations, and sea-to-air fluxes.

Season	Area	Time	T (°C)	S	DO%	Surface CH_4 Conc. (nM)	Wind Speed (m/s)	CH_4 Sea-to-Air Fluxes (μmole m^{-2} h^{-1})	(μmole m^{-2} d^{-1})
SPRING 2022 (2022/5/19-22)	Seagrass Water	day	28.3 ± 1.0	32.78 ± 0.29	118.6 ± 13.6	6.6 ± 1.1	3.2	0.14 ± 0.04	
		night	26.1 ± 0.7	32.51 ± 0.55	87.0 ± 12.8	13.1 ± 12.3		0.31 ± 0.35	
		seasonal	27.2 ± 1.6	32.64 ± 0.19	102.8 ± 22.3	9.9 ± 4.6			5.4 ± 3.0
	Coastal Water	day	28.7 ± 0.9	33.27 ± 0.47	107.5 ± 5.3	5.4 ± 0.8		0.10 ± 0.02	
		night	26.3 ± 0.7	32.86 ± 0.30	98.2 ± 2.8	5.4 ± 1.0		0.09 ± 0.03	
		seasonal	27.5 ± 1.7	33.06 ± 0.29	102.8 ± 6.6	5.4 ± 0.0			2.3 ± 0.1
SUMMER 2023 (2023/6/13-17)	Seagrass Water	day	28.8 ± 0.9	31.83 ± 0.63	109.3 ± 18.5	7.6 ± 3.2	2.2	0.08 ± 0.05	
		night	28.5 ± 0.7	32.04 ± 0.26	88.5 ± 9.5	11.1 ± 5.3		0.13 ± 0.08	
		seasonal	28.7 ± 0.2	31.94 ± 0.15	98.9 ± 14.7	9.3 ± 4.2			2.5 ± 0.8
	Coastal Water	day	29.0 ± 1.0	32.14 ± 0.60	100.5 ± 5.0	5.5 ± 2.3		0.05 ± 0.03	
		night	28.9 ± 0.8	32.10 ± 0.06	99.3 ± 2.2	4.2 ± 1.2		0.03 ± 0.02	
		seasonal	29.0 ± 0.0	32.12 ± 0.03	99.9 ± 0.8	4.9 ± 0.9			0.9 ± 0.3
AUTUMN 2022 (2022/9/27-30 - 2022/10/1-2)	Seagrass Water	day	30.0 ± 1.5	32.93 ± 0.12	124.4 ± 22.0	8.3 ± 2.7	2.6 - 5.4	0.37 ± 0.27	
		night	28.3 ± 0.6	32.83 ± 0.29	94.5 ± 7.0	6.9 ± 2.0		0.19 ± 0.20	
		seasonal	29.1 ± 1.2	32.88 ± 0.07	109.4 ± 21.1	7.6 ± 1.0			6.8 ± 3.1
	Coastal Water	day	29.6 ± 1.3	33.02 ± 0.15	105.6 ± 7.6	7.4 ± 6.2		0.36 ± 0.58	
		night	29.2 ± 0.2	32.91 ± 0.11	97.0 ± 0.9	4.5 ± 0.6		0.05 ± 0.01	
		seasonal	29.4 ± 0.3	32.97 ± 0.08	101.3 ± 6.1	6.0 ± 2.1			4.9 ± 5.2
Seasonal Average	**Seagrass Water**								**4.9 ± 2.2**
	Coastal Water								**2.7 ± 2.0**

Table 2. Seasonal variations in-situ benthic chamber incubations of CH_4 production rates and sediment-to-water fluxes.

Season	Sampling date	Habitat	Production Rates			Sediment-to-water flux		
			day	night	seasonal	day	night	seasonal
			(μmole m^{-3} h^{-1})		(μmole m^{-3} d^{-1})	(μmole m^{-2} h^{-1})		(μmole m^{-2} d^{-1})
SPRING	May,19-22, 2022	**seagrass**	3.7 ± 0.7	4.9 ± 3.9	102.9 ± 20.5	1.5 ± 0.3	2.0 ± 1.5	41.2 ± 8.2
		sand	2.1 ± 0.6	1.4 ± 0.9	42.1 ± 11.1	0.8 ± 0.2	0.6 ± 0.4	16.9 ± 4.5
SUMMER	Jun. 13-17, 2023	**seagrass**	11.3 ± 7.0	13.3 ± 14.1	295.0 ± 35.1	4.5 ± 2.8	5.3 ± 5.6	118.0 ± 14.0
		sand	3.8 ± 7.6	5.7 ± 9.8	114.0 ± 30.6	1.5 ± 3.0	2.3 ± 3.9	45.6 ± 12.2
AUTUMN	Sep. 27-Oct. 2, 2022	**seagrass**	11.0 ± 29.6	N/A	263.3 ± 710.4	4.4 ± 11.8	N/A	105.3 ± 284.2
		sand	40.5 ± 39.9	N/A	972.2 ± 957.1	16.2 ± 16.0	N/A	388.9 ± 382.8
Seasonal Average		**seagrass**			**220.4 ± 103.0**			**88.2 ± 41.2**
		sand			**376.1 ± 517.5**			**150.4 ± 207.0**

Table 3. The global CH_4 sea-to-air and sediment-to-water fluxes

Location	Species	Site	Climate	Water Depth (m)	Method	Sea-to-air Flux ($\mu mol\ m^{-2}d^{-1}$)	Method	Sediment-to-water Flux ($\mu mol\ m^{-1}d^{-1}$)	References
Wallagoot, Australia	*Ruppia megacarpa*	Mouth of estuary	Temperate	0.8	Continuous surface water	33.8			
	Halophila ovalis			1.7				45.4	(Camillini, 2020)
Wallis Lake, Australia	*Posidonia australis*	Mouth of estuary	Temperate	1.2			Benthic chamber	279.3	
	Zostera muelleri			0.9				46.0	
Swan Bay, Australia	*Zostera muelleri*	Tidal lagoon	Temperate	-	Continuous surface water	10.5			(Olivé et al., 2016)
South Bay, Virginia, USA	*Zostera marina*	Coastal bay with marsh	Temperate	-			Benthic chamber	136.7 ± 127.8	(Oreska et al., 2020)
East Harbor, Massachusetts, USA	*Zostera marina*	Lagoon-marsh	Temperate	1	Discrete water samples	107.5	Benthic chamber	0.0	(Al-Haj et al., 2022)
Pleasant Bay, Massachusetts, USA	*Zostera marina*	Coastal lagoon	Temperate	2		113.8		73.3	
Cadaques, Spain	*Posidonia oceanica*	Coastal bay	Temperate	2-10	Continuous surface water	0.1 ± 0.1	Porewater samples	0.3 ± 0.1	(Yau et al., 2023)
Ria Formosa Lagoon, Portugal	*Zostera noltii*	Coastal lagoon	Temperate	Intertidal zones	Dynamic flux chamber	307.2			(Bahlmann et al., 2015)
Baltic Sea, Finland	*Zostera marina*	Coastal bay	Temperate	2				1.6 ± 1.6	
Kattegat, Denmark	*Zostera marina*	Fjord-coastal Bay	Temperate	2			Benthic chamber	3.4 ± 0.5	(Asplund et al., 2022)
Skagerrak, Sweden	*Zostera marina*	Coastal bay	Temperate	2.2				2.5 ± 2.8	
Mediterranean Sea, Italy	*Posidonia oceanica*	Coastal bay	Temperate	NA			Porewater	106.0	(Schorn et al., 2022)
Swan lake, Shandong, China	*Zostera marina, Zostera japonica*	Coastal lagoon	Temperate	0.5-1.5	Water samples	5.5 ± 8.4			(Tan et al., 2025)
	Enhalus acoroides							96.2	
	Thalassodendron ciliatum							3.2	
	Halophila decipiens							1.4	
Red Sea, Saudi Arabia	*Thalassia hemprichii*	Coastal inlet	Tropical	Shallow shelves			Core incubation	6.5	(Garcias-Bonet and Duarte, 2017)
	Halophila, Halodule spp.							61.0	
	Halodule uninervis							48.1	
	Cymodocea serrulate, Halodule uninervis							401.3	
Chilika Lagoon, India	*Halodule sp., Halophila sp*	Tidal lagoon	Tropical	0.9–2.6	Discrete water samples	120.0			(Banerjee et al., 2018)
Awerange Bay, Indonesia	*Enhalus acoroides*	Coastal bay	Tropical	14			Sediment core	95.7 ± 95.4	(Alongi et al., 2008)
Koh Mook, Thailand	*Enhalus acoroides*	Coastal inlet	Tropical	Intertidal zones	Benthic chamber	3.1			(Halim et al., 2024)
	Thalassia hemprichii					2.0			
Haikou, Taiwan	*Thalassia hemprichii, Halodule pinifolia*	Coastal inlet	Tropical	0.5-1.5	Discrete water samples	4.9 ± 2.2	Benthic chamber	88.2 ± 41.2	This study

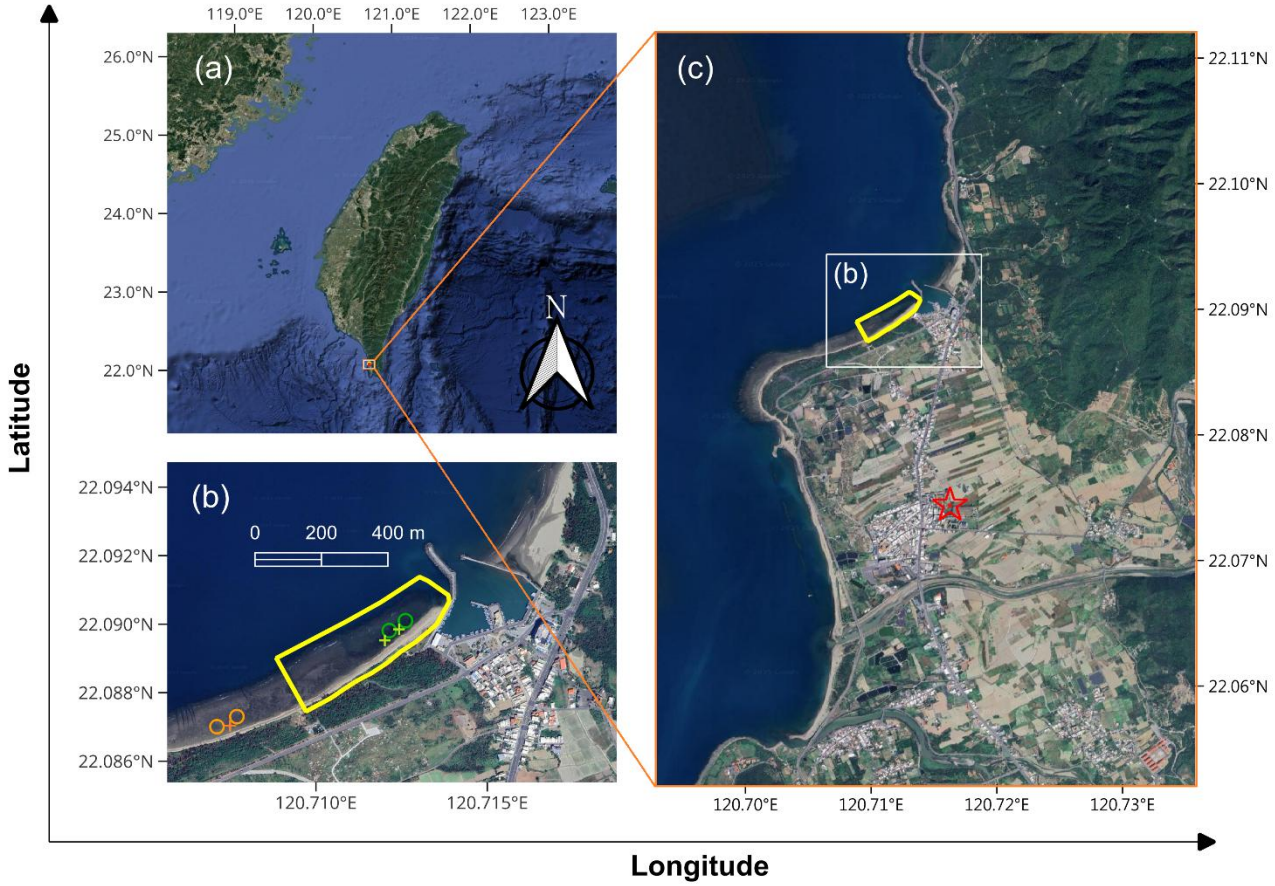

Figure 1. Study area. (a) Regional map showing the location of the study area. (b) Close-up view of the benthic chamber incubation sites. The yellow rectangle outlines the Haikou seagrass meadow and the red star indicates the location of the Checheng Weather Station. (c) Zoomed-in map of the study area. Green circles (◯) indicate chamber incubation sites in the seagrass area, while orange circles (◯) indicate chamber incubation sites in the bare sand area. Green crosses (+) indicate porewater sampling sites in the seagrass area, while orange cross (+) indicates porewater sampling sites in the bare-sand area.

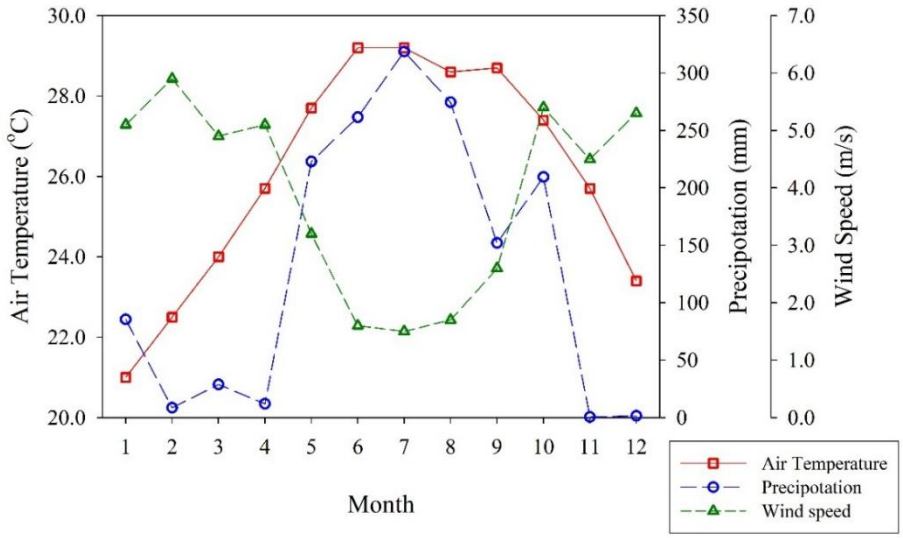

Figure 2. Monthly mean air temperature, total precipitation, and mean wind speed recorded at the Checheng Weather Station (see Figure 1 for location) during 2022–2023.

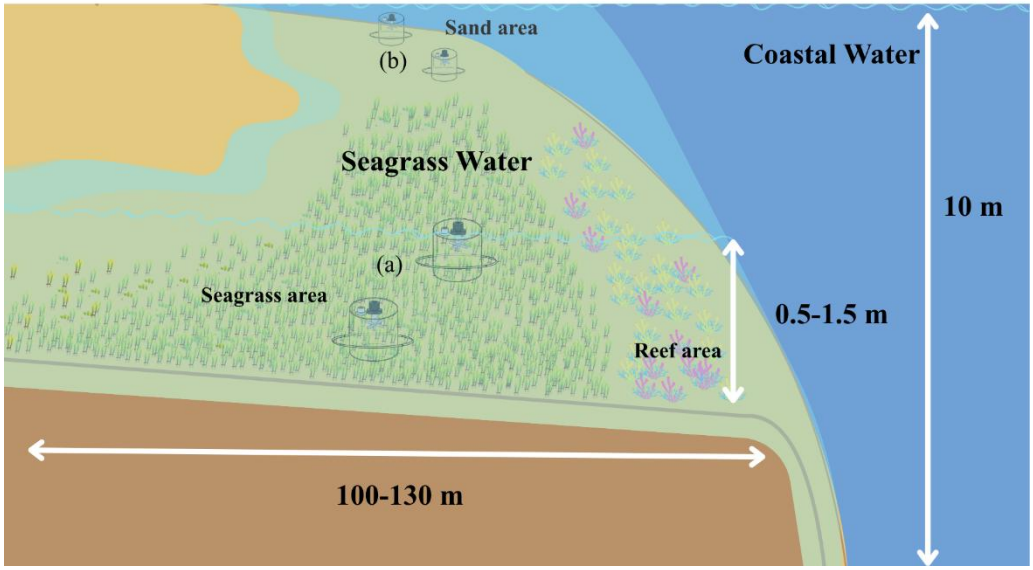

Figure 3. Conceptual diagram illustrating the geographic setting of the study area, including the seagrass meadow, adjacent bare sand area, reef platform, and coastal water site. The dark blue shaded area represents the adjacent coastal waters, where the water depth was approximately 10 m, whereas the light blue shaded area represents the shallow seagrass and bare-sand areas, where the water depth was approximately 0.5–1.5 m. Labels (a) and (b) indicate the benthic chamber incubation sites in the seagrass and bare sand areas, respectively; photographs of the corresponding chamber deployments are shown in Figures 4a and 4b.

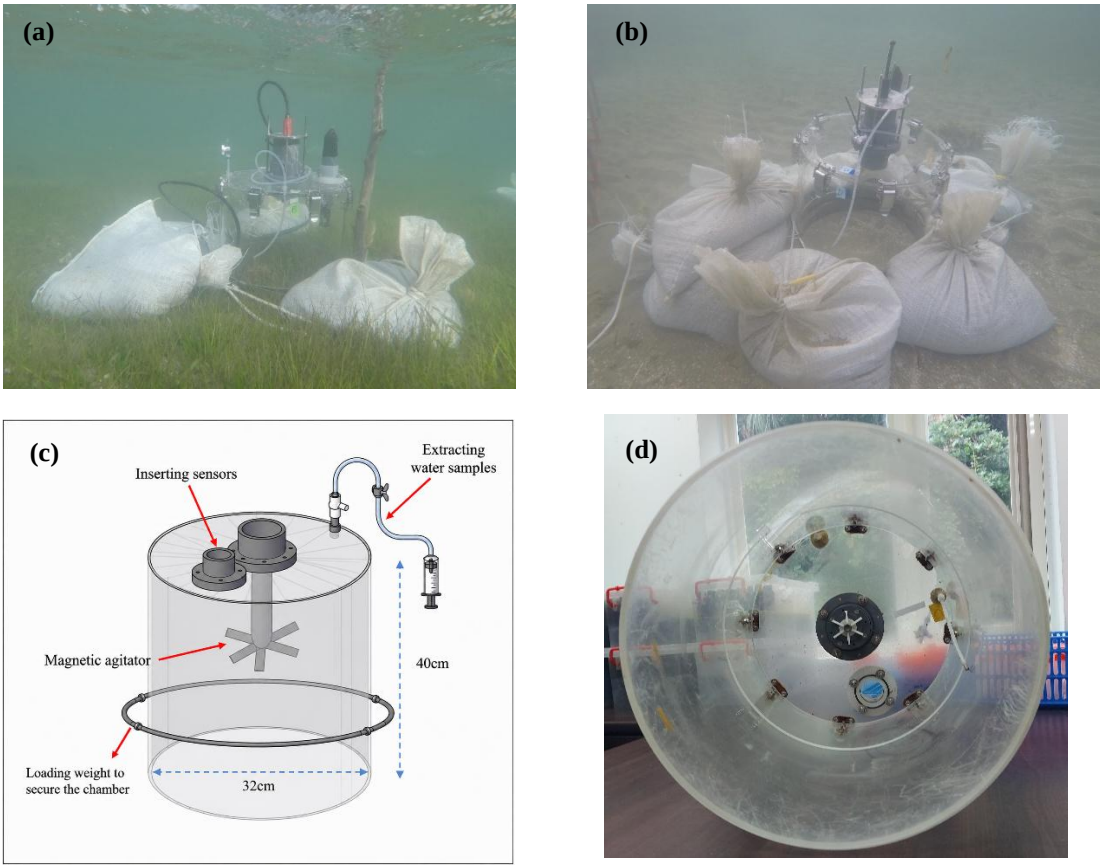

Figure 4. In situ benthic chamber incubation system deployed in (a) the seagrass meadow and (b) adjacent bare sediment, with (c) a schematic illustration of the chamber design and (d) an upward view from inside the chamber.

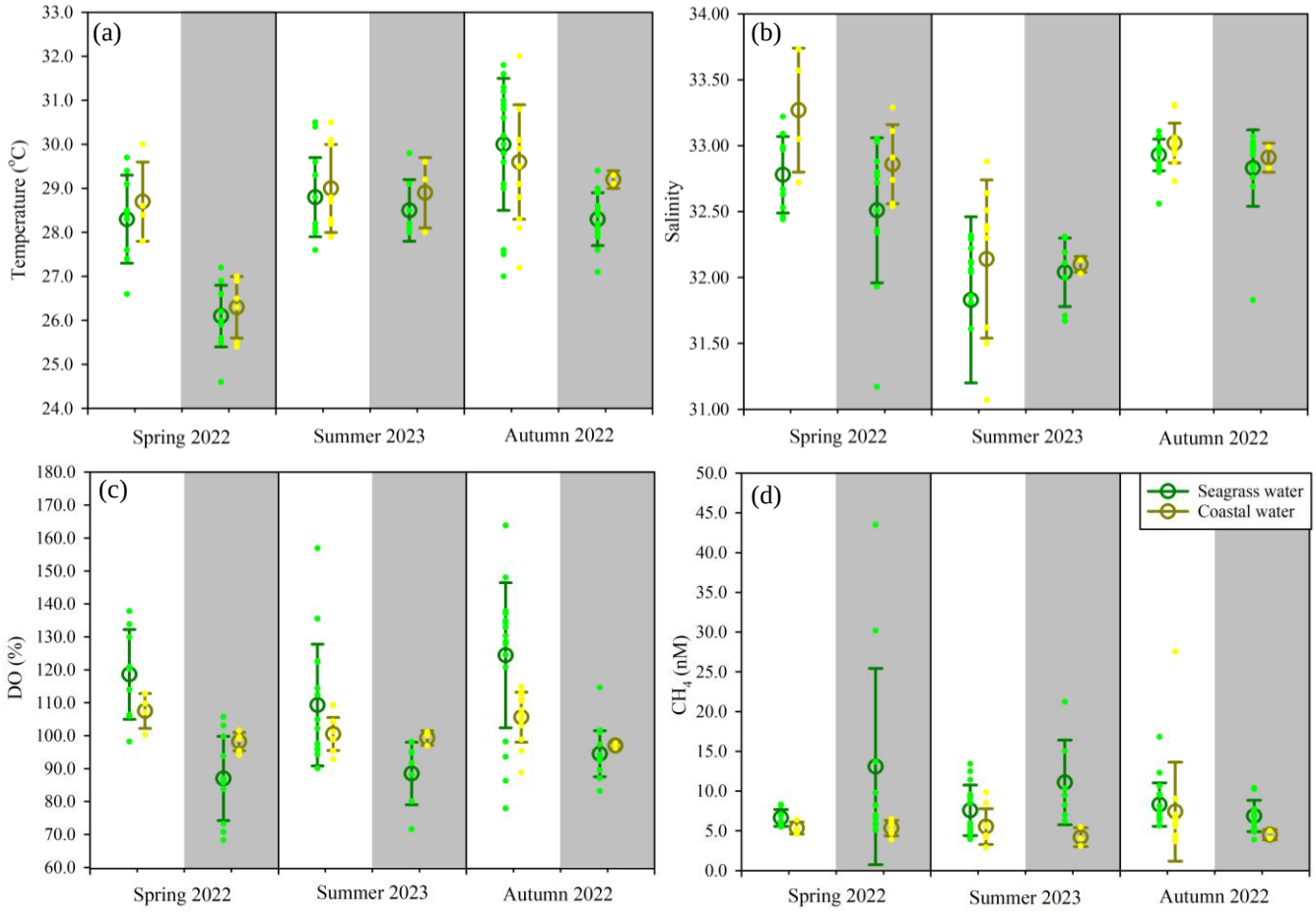

Figure 5. Seasonal environmental conditions of (a) temperature, (b) salinity, (c) DO%, and (d) CH_4 concentrations in surface seagrass water and coastal water. Bright areas indicate daytime, and grey areas indicate nighttime.

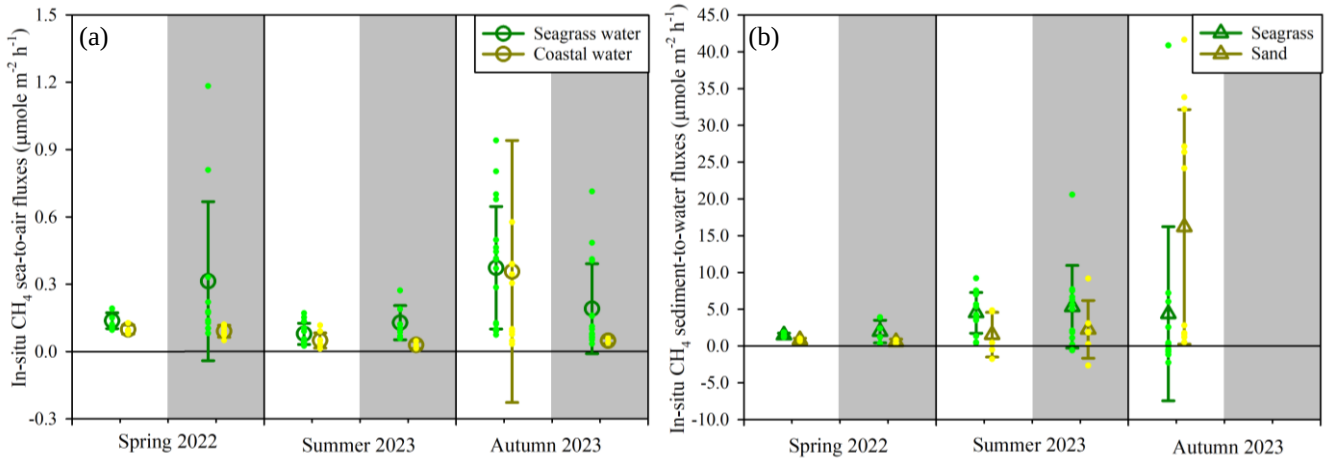

Figure 6. Diurnal variation of CH_4 (a) sea-to-air fluxes (µmole m^{-2} h^{-1}; n=226) in surface water of the seagrass meadow and adjacent coastal water, and (b) sediment-to-water fluxes (µmole m^{-2} h^{-1}; n=284) from seagrass and bare sand sediments. Bright areas indicate daytime, and grey areas indicate nighttime.

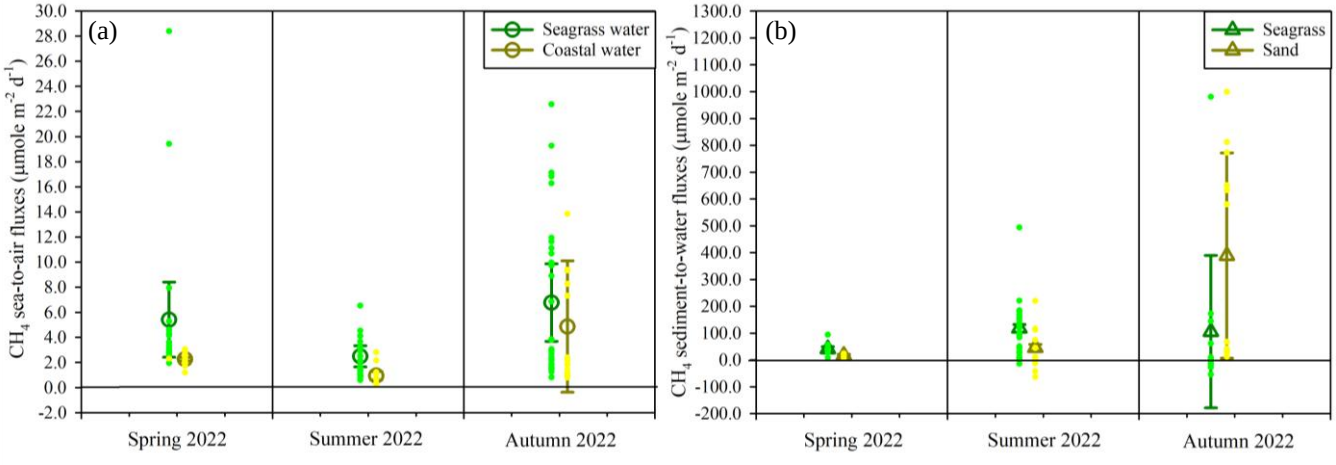

Figure 7. Seasonal variation of CH_4 (a) sea-to-air fluxes (µmole m^{-2} d^{-1}; n=226) in surface water of the seagrass meadow and adjacent coastal water, and (b) sediment-to-water fluxes (µmole m^{-2} d^{-1}; n=284) from seagrass and bare sand sediments.

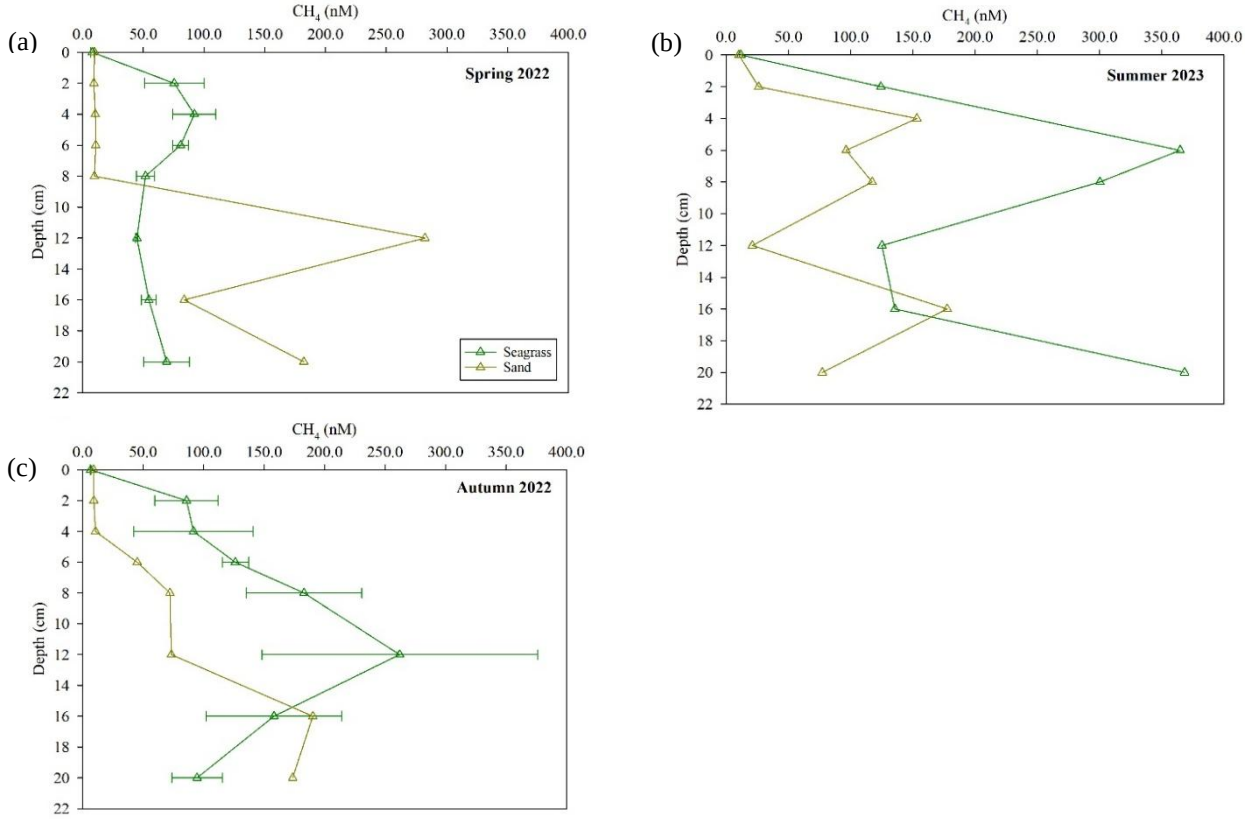

Figure 8. CH_4 concentration profiles in porewater: (a) spring 2022 (n=32), (b) summer 2023 (n=15), and (c) autumn 2022 (n=32). Error bars represent the range of duplicate samples; error bars are absent for depth intervals where only single sample was available.