

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

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Abstract. ~~This study provides the first integrated assessment of diel, seasonal, and annual methane (CH₄) dynamics in Taiwan's seagrass ecosystems, focusing on the Haikou seagrass meadow and adjacent coastal waters. From May 2022 to June 2023, field campaigns combined surface water sampling, in situ benthic chamber incubations and porewater profiling in both seagrass and bare sand habitats to evaluate CH₄ fluxes at the sediment–water and water–air interfaces. Results showed similar temperature and salinity patterns between seagrass and coastal waters, but seagrass habitats exhibited strong diurnal oxygen fluctuations that suppressed daytime CH₄ accumulation. Seagrass habitats consistently had higher CH₄ concentrations and sea-to-air fluxes than other coastal area, with nighttime emissions exceeding daytime values and autumn fluxes peaking under windy conditions. Sediment incubations identified benthic processes as the dominant CH₄ source. Seagrass sediments sustained relatively stable fluxes across seasons, while sandy sediment produced episodic pulses during storm events. Porewater profiles revealed elevated CH₄ in the upper 12 cm of sediments, especially in seagrass, with declines at depth due to substrate limitation and anaerobic oxidation. At the ecosystem scale, the Haikou seagrass meadow emitted approximately 78.3 mol CH₄ yr^{−1} to the atmosphere from the water column, while sediments released 1,410.1 mol CH₄ yr^{−1} into the water column, 94% of which was oxidized before reaching the atmosphere or transported laterally. These fluxes are ecologically significant, emphasizing the dual role of seagrass meadows as carbon sinks and localized sources of CH₄ within tropical coastal ecosystems in Taiwan.~~

Seagrass meadows are important blue carbon ecosystems that sequester large amounts of organic carbon but can also emit methane (CH₄), potentially offsetting part of their climate mitigation benefits. However, the seasonal and diurnal dynamics of CH₄ production and emissions in tropical seagrass ecosystems remain poorly understood. This study presents the first integrated assessment of CH₄ 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 CH₄ dynamics at both the sediment-to-water and sea-to-air interfaces. The seagrass meadow consistently exhibited higher dissolved CH₄ concentrations and sea-to-air CH₄ fluxes

than adjacent coastal waters, confirming that it functions as a localized atmospheric CH₄ hotspot. Nighttime dissolved CH₄ concentrations generally exceeded daytime values, reflecting diurnal variations in oxygen availability, whereas seasonal variability in sea-to-air CH₄ fluxes was primarily driven by wind speed. Mean sediment-to-water and sea-to-air CH₄ fluxes were 88.2 ± 41.2 and 4.9 ± 2.2 $\mu\text{mol m}^{-2} \text{d}^{-1}$, respectively. Despite substantial benthic CH₄ production, atmospheric emissions remained comparatively low, indicating a marked decoupling between sediment-to-water and sea-to-air CH₄ fluxes. This decoupling suggests that much of the sediment-derived CH₄ was transported laterally by tidal exchange and coastal circulation before atmospheric release, with microbial oxidation acting as an additional sink. Compared with adjacent sandy sediments, seagrass sediments consistently maintained higher baseline CH₄ production rates and benthic fluxes owing to greater organic matter availability and favorable microbial conditions, whereas unvegetated sandy sediments generally exhibited low CH₄ production but produced episodic CH₄ pulses following storm-induced sediment disturbance. Elevated porewater CH₄ concentrations during summer and autumn further indicated enhanced methanogenesis associated with organic matter accumulation under calmer hydrodynamic conditions. Overall, these findings demonstrate that CH₄ cycling in tropical seagrass meadows is jointly regulated by biological processes and hydrodynamic conditions, highlighting the need to consider both CH₄ 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. As a result, atmospheric concentrations of carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) have risen substantially. By trapping heat in the Earth's atmosphere through the greenhouse effect, these gases play a central role in driving global warming and ongoing climate change. As a result, global surface temperatures rose to 1.1°C above 1850–1990 levels during the period 2011–2020, driving global warming and ongoing climate change (IPCC, 2021). Achieving climate neutrality requires both not only reducing GHG emissions but also protecting and enhancing natural GHG carbon sinks. Additionally, long-term carbon storage is necessary to offset unavoidable residual emissions. One effective strategy for countries is to preserve and expand 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, such as including mangroves, seagrasses, and salt marshes, store substantial amounts of carbon in their sediments and play a vital critical role by sequestering large amounts of organic carbon in their sediments, in climate change mitigation. These ecosystems are collectively known as "Blue Carbon ecosystems". 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 serve as vital blue carbon reservoirs in coastal ecosystems, playing a crucial role in climate mitigation due to their exceptional capacity for carbon capture and storage (Lovelock and Duarte, 2019; McLeod et al., 2011; Rosentreter et al., 2021b; 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.

As some of the world's most significant carbon sinks, seagrass meadows accumulate substantial organic matter from both allochthonous and autochthonous sources, further enhancing their role in global carbon storage (McLeod et al., 2011). However,

Despite these benefits, ecosystems seagrass meadows are also recognized as sources of methane (CH_4), a potent GHG with a sustained-flux global warming potential (SGWP) 27–80.96 times greater than that of 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 regions and geography, CH_4 emissions from seagrass meadows could may offset up to -0.5–33.4% of the blue carbon sequestered in sediments (Eyre et al., 2023; Rosentreter et al., 2021b; Yau 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 $\text{Tg CH}_4 \text{ yr}^{-1}$ through ebullition alone is a global hotspot for CH_4 emissions, accounting for 75% of oceanic CH_4 emissions (Weber et al., 2019), with continental shelves alone contributing approximately 13 $\text{Tg CH}_4 \text{ yr}^{-1}$.

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 (Arndt et al., 2013; Oreska et al., 2020; Saunois et al., 2020; Schorn et al., 2022; Sogin et al., 2022). 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 (Howard et al., 2023; Kuwae et al., 2022).

While methanogenesis is traditionally believed to be suppressed by sulfate reduction in saline environments, studies have shown that it can persist concurrently with sulfate reduction in sulfate-rich anoxic sediments (Lyimo et al., 2018). This is likely

due to the availability of non-competitive substrates, such as methylamines and methanol, which serve as alternative carbon sources for methanogens (Reeburgh, 2007). Although aerobic CH_4 production in seagrass meadows is considered a minor pathway (Schorn et al., 2022), the CH_4 generated in sediments can be released into the overlying water column via diffusion or advective exchange, potentially contributing to CH_4 emissions from these ecosystems (Saunois et al., 2020). Seagrass meadows are vital to coastal carbon cycling, but their function as CH_4 sources adds complexity to evaluating their overall climate impact. While some studies suggest that seagrass meadows generally emit less CH_4 compared to mangroves and salt marshes (Yau et al., 2023), site-specific conditions can lead to substantial variability in emissions (Oreska et al., 2020). CH_4 production in seagrass meadows is driven by various biogeochemical processes, including organic matter decomposition, microbial interactions, and sedimentary conditions, which influence the balance between carbon sequestration and CH_4 emissions (Arndt et al., 2013; Saunois et al., 2020; Schorn et al., 2022; Sogin et al., 2022). Given that CH_4 is a potent GHG capable of offsetting some of the climate benefits of seagrass carbon storage, accurately quantifying seagrass-associated CH_4 fluxes is essential for assessing their net climate impact. Integrating these emissions into both local and global CH_4 budget assessments is crucial for a comprehensive understanding of seagrass meadows' role in climate regulation. This understanding is particularly important as seagrass conservation and restoration efforts are increasingly incorporated into carbon credit systems and global climate strategies, such as the Paris Agreement and voluntary carbon markets (Kuwae et al., 2022). Effectively managing these dynamics will be key to maximizing the climate benefits of seagrass ecosystems while ensuring their inclusion in sustainable carbon mitigation policies (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 diel, seasonal, and annual CH_4 dynamics in the Haikou seagrass meadow, southern Taiwan, a seagrass ecosystem, with a focus on the Haikou seagrass meadow. Through three a series of intensive field campaigns, we combining ed surface water sampling, in situ benthic chamber incubations, and porewater profiling, we to quantified investigate CH_4 production and fluxes processes in both seagrass and adjacent bare sandy sediments across the sediment-to-water and water-to-air interfaces, habitats. 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.

allowed us to capture patterns of CH_4 variability across multiple temporal scales and environmental settings, thereby quantifying fluxes at the sediment-water and water-air interfaces and offering new insights into the role of seagrass meadows in coastal carbon cycling.

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*—*Halophila pinifolia*. This natural subtidal seagrass meadow is home to several seagrass species, including *Thalassia hemprichii* and *Halophila pinifolia*, covering an area of approximately 4.38 ha (Lin et al., 2023). During the study period, seagrass cover ranged from 45% to 90%, with a mean cover of 66%. Water depth at the study site 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. Water depth at the site varies with the tide, ranging from approximately 0.5 m at low tide to 1.5 m at high tide. Beyond the seagrass meadow lies a reef platform, and further offshore the depth increases to about 10 m, referred to as coastal water in this study. Field investigations were conducted simultaneously within the Haikou seagrass meadow and in adjacent bare sand areas without seagrass. Both sites are located in the intertidal zone and experience similar tidal depth variations. Samples were collected, and in situ incubations were conducted from May 19 to 23 (spring) and September 26 to October 4 (autumn) in 2022, as well as and from June 13 to 17 (summer) in 2023. Due to severe winter weather conditions, in situ incubations could not be performed. In situ cultivation experiments were conducted in different seasons, both during the day and at night, to examine diurnal and seasonal fluctuations in CH₄ fluxes at the sediment-water and water-air interfaces in response to changing environmental conditions. 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 water-to-air CH₄ 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 CH₄ 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, samples collection and chemical analysis

In situ benthic cultivation experiments were conducted at four sites, including two seagrass meadow sites (Figure 2a) and two bare sand sites (Figure 2b), 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 2c). 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. All experiments were performed in duplicate.

The in situ benthic cultivation experiments were conducted during both day and night for approximately 2 to 5 hours, depending on wave and weather conditions as well as operational constraints. Specifically, although a standard 5-hour sampling interval was intended, poor weather conditions occasionally restricted diver deployment, resulting in shorter incubation periods, sampling needs, wave conditions, and weather. To ensure continuous water circulation, a magnetic agitator was positioned inside the chamber (Figure 4d). To simulate natural water movement, a magnetic agitator was placed above the chamber. Water samples were collected using a three-way valve installed on the incubator, while temperature, salinity, and dissolved oxygen (DO) were measured simultaneously. Meanwhile, surface seawater samples were collected seven times a day from seagrass bed areas at 06:00, 09:00, 12:00, 15:00, 18:00, 21:00 and 24:00. Additionally, samples were collected from coastal waters outside the reef platforms at the same times, except for 21:00 and 24:00, due to safety concerns.

2.3 Samples collection and chemical analysis

~~Seaw~~ Water samples for CH₄ analysis were collected in duplicate at a depth of approximately 0.5 m 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 (HgCl₂) 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 used 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). ~~from both seagrass beds and nearby sand areas using porewater wells and a Luer-Lok syringe at sediment depths of 0, 2, 4, 6, 8, 12, 16, and 20 cm (Falter and Sansone, 2000), then~~ Sample were immediately transferred into 30 mL brown serum bottles, preserved with 50 µL HgCl₂, sealed with butyl rubber stoppers and aluminum caps, placed on ice in a dark cooler during transport, ~~transported to the lab,~~ and stored in darkness at 4 °C until analysis. Porewater samples were collected once daily from both the seagrass meadow and bare sand sediments at locations independent of 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 the time of sampling, water temperature, pH, salinity, and DO were measured on-site using a portable multiparameter water quality meter (YSI ProDSS, USA). Dissolved CH₄ 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).

2.4.2.3 The CH₄ saturation ratio and water-air fluxes

The CH₄ saturation ratio (R, %) was determined using the formula:

$$R = (C_{\text{obs}}/C_{\text{eq}}) \times 100, \tag{1}$$

where C_{obs} represents the observed concentration of dissolved CH₄ in seawater, and C_{eq} denotes the expected equilibrium concentration. The equilibrium CH₄ concentration was estimated using the solubility equation of Wiesenburg and Guinasso

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(1979), incorporating in-situ temperature, salinity, and atmospheric CH₄ molar fractions. Atmospheric CH₄ data for May, September, and October 2022, along with June 2023, were sourced from the NOAA Global Monitoring Laboratory (Lan, 2024).

CH₄ fluxes at the sea–air interface were calculated using the equation:

$$F_{\text{sea-air}} = k \times (C_{\text{obs}} - C_{\text{eq}}) \tag{2}$$

where k, the gas exchange coefficient, was determined following Wanninkhof (2014):

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

Here, Sc is the Schmidt number for CH₄, 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.

2.5.2.4 The benthic CH₄ production rates and sediment-water fluxes

Benthic production rates and 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. We estimated the benthic production rates and fluxes of sediment water–interface in in-situ incubation with this following formula:

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

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

where F_{sediment-water} is sediment–water flux (μmol m⁻² h⁻¹ or μmol m⁻² d⁻¹); ΔC represent the differences in CH₄ concentration (nmol L⁻¹), during the incubation period Δt (hours); V_{chamber} is the volume of overlying water in the chamber (m³); A_{chamber} is the area of the chamber (m²).

3. Results and Discussion

3.1 Seasonal and diurnal variability in surface water conditions

Seasonal surface water conditions in seagrass and coastal areas were generally similar across spring 2022, autumn 2022, and summer 2023. Surface temperatures ranged from 24.6 to 32.0 °C, with seasonal averages of 27.1–29.2 °C in seagrass water and 27.2–29.6 °C in coastal water (Table 1). Daytime temperatures were consistently higher than nighttime, particularly in seagrass areas (Fig. 3a). Salinity ranged from 30.21 to 33.73, with slightly lower seasonal averages in seagrass water (31.90–32.88) compared to coastal water (32.13–33.02; Fig. 3b), likely due to freshwater input. DO saturation in seagrass water showed strong diurnal variation, increasing from nighttime averages of 87.0–94.5% to daytime levels of 109.3–124.4% (Fig. 3c), driven by seagrass photosynthesis. Coastal water DO saturation was more stable, with seasonal averages of 100.2–104.5%, slightly lower than those in seagrass water (101.2–110.3%; Table 1).

Dissolved CH₄ concentrations in seagrass waters exhibited clear seasonal and diurnal variability, with higher averages at night and lower values during the day, except in autumn 2022 when a severe weather event disrupted this pattern. The daytime suppression of CH₄ was likely associated with elevated dissolved oxygen saturation driven by photosynthesis. Coastal waters exhibited lower and more stable CH₄ concentrations than seagrass waters. Seasonal averages ranged from 5.2 to 7.0 nM in coastal waters, consistently below the values observed in seagrass waters of 7.6 to 10.2 nM as shown in Table 1. This difference likely reflects the greater depth of the coastal waters at approximately 10 m, which reduces sediment influence compared with the much shallower seagrass habitats that range from about 0.5 to 1.5 m in depth. Alternatively, CH₄ released from sediments may have been oxidized before reaching the coastal water surface.

Daytime and nighttime mean temperatures ranged from 28.3–30.0 °C and 26.1–28.5 °C, respectively, in the seagrass meadow, and from 28.7–29.6 °C and 26.3–29.2 °C, respectively, in the coastal water. Seasonal mean temperatures ranged from 27.2 to 29.1 °C in the seagrass meadow and from 27.5 to 29.4 °C in the coastal water (Table 1). Daytime surface water temperatures were consistently higher than nighttime temperatures, with a more pronounced diurnal difference in the seagrass meadow than in the coastal water (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 coastal water (32.12–33.06; Figure 5b). 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 CH₄ concentrations and sea-to-air CH₄ fluxes

Sea-to-air CH₄ fluxes from both seagrass and coastal waters showed distinct spatial and temporal patterns, modulated by CH₄ concentrations and wind speed. Monthly average wind speeds at Checheng Weather Station were 3.2 m/s in spring 2022, 2.6–5.4 m/s in autumn 2022, and 2.2 m/s in summer 2023 (Table 1). Given the consistently higher CH₄ concentrations in seagrass waters and the effect of wind on gas exchange, CH₄ fluxes were generally greater in seagrass habitats across all seasons and times of day (Fig. 4a). In both environments, the highest CH₄ sea-to-air fluxes occurred in autumn 2022, with average fluxes of $6.8 \pm 3.1 \mu\text{mole m}^{-2} \text{d}^{-1}$ in seagrass waters and $4.9 \pm 5.2 \mu\text{mole m}^{-2} \text{d}^{-1}$ in coastal waters. These were followed by lower fluxes in spring 2022 and summer 2023 (Fig. 5a), a pattern that likely reflects seasonal differences in wind speed (Table 1). The observed CH₄ enrichment in seagrass waters supports the hypothesis that seagrass meadows act as localized CH₄ hotspots, contributing significantly to GHG fluxes in coastal zones. Elevated concentrations and fluxes indicate that seagrass beds not only accumulate CH₄ but also actively release it into the overlying water, likely driven by sedimentary methanogenesis and upward transport processes. Unlike open water environments, seagrass plants possess specialized tissues such as aerenchyma that facilitate internal gas transport. While these structures enhance oxygen exchange, they can also act as conduits for CH₄ to escape from sediments into the water column (Yau et al., 2023), potentially increasing CH₄ emissions in seagrass habitats.

These enhanced fluxes may result from increased microbial activity, greater organic matter input, and reduced oxygen penetration within the seagrass rhizosphere (Henriksson et al., 2024). Collectively, these results highlight the role of seagrass ecosystems as critical biogeochemical hotspots for CH₄ production and release, with important implications for coastal GHG budgets and climate mitigation strategies.

Mean surface CH₄ concentrations were consistently 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 CH₄ 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 CH₄ fluxes exhibited distinct spatial and seasonal patterns, influenced by both surface CH₄ concentrations and wind speed. Monthly mean wind speeds recorded at the Checheng Weather Station were 3.2 m s⁻¹ in spring 2022, 2.6–5.4 m s⁻¹ in autumn 2022, and 2.2 m s⁻¹ in summer 2023 (Table 1). Correspondingly, CH₄ fluxes were consistently 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 CH₄ fluxes occurred in autumn 2022, averaging $6.8 \pm 3.1 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the seagrass meadow and $4.9 \pm 5.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the coastal water (Figure 7a). In spring 2022, mean CH₄ fluxes decreased to $5.4 \pm 3.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the seagrass meadow and $2.3 \pm 0.1 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the coastal water (Figure 7a). The lowest fluxes were observed in summer 2023, averaging $2.5 \pm 0.8 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the seagrass meadow and $0.9 \pm 0.3 \mu\text{mol m}^{-2} \text{d}^{-1}$ 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 sediment CH₄ dynamics and sediment-to-water production rates and benthic fluxes

Seasonal averages CH₄ production rates in seagrass sediments were 102.9 ± 20.5 in spring 2022, 263.3 ± 710.4 in autumn 2022, and $295.0 \pm 35.1 \mu\text{mol m}^{-3} \text{d}^{-1}$ in summer 2023 (Table 2). The corresponding sediment to water fluxes were 41.2 ± 8.2 , 105.3 ± 284.2 , and $118.0 \pm 14.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ (Fig. 5b). In sandy sediments, the values were lower in spring at $42.1 \pm 11.1 \mu\text{mol m}^{-3} \text{d}^{-1}$ and the sediment to water flux was $16.9 \pm 4.5 \mu\text{mol m}^{-2} \text{d}^{-1}$. In summer, the production rate was $114.0 \pm 30.6 \mu\text{mol m}^{-3} \text{d}^{-1}$ and the sediment to water flux was $45.6 \pm 12.2 \mu\text{mol m}^{-2} \text{d}^{-1}$. However, both production rates and sediment to water fluxes increased sharply in autumn to $972.2 \pm 957.1 \mu\text{mol m}^{-3} \text{d}^{-1}$ and $388.9 \pm 382.8 \mu\text{mol m}^{-2} \text{d}^{-1}$. Overall, CH₄ production rates and fluxes in seagrass sediments remained relatively stable, whereas sandy sediments showed episodic peaks associated with storm events.

In-situ benthic chamber incubations showed that CH₄ production rates and fluxes were higher in seagrass sediments than in sandy sediment during both daytime and nighttime in spring 2022 and summer 2023 (Fig. 4b). According to Liang et al. (2025), a higher abundance of methanogenic archaea in seagrass sediments compared to adjacent unvegetated areas, indicating elevated CH₄ production potential within seagrass ecosystems. These findings suggest that while seagrass beds are important carbon sinks, they may also act as localized CH₄ sources, potentially offsetting some of their climate mitigation benefits. In contrast, autumn 2022 presented an exception: values in seagrass sediment fell below those of sandy sediment during the

daytime (Fig. 4b), while nighttime data were unavailable due to heavy rainfall. This anomaly was likely caused by heavy rain and strong winds that disturbed the sandy sediments and enhanced CH₄ release, whereas seagrass typically stabilizes sediments and buffers against such disturbances.

Seagrass meadows accumulate substantial organic carbon, which provides a substrate for methanogenesis. The decomposition of seagrass detritus enhances microbial activity, thereby increasing CH₄ production (Schorn et al., 2022). Dense seagrass stands create anoxic sediment environments where methanogenic archaea thrive, promoting higher CH₄ production compared to the more oxygenated conditions of sandy sediments (Sademe et al., 2023). This elevated activity is linked to the accumulation of organic matter, reduced oxygen penetration, and active microbial communities within the rhizosphere (Sogin et al., 2022). In contrast, sandy sediments generally exhibited only moderate CH₄ production rates, likely due to lower organic content and limited microbial activity, except during a severe weather event that disturbed the sediments and enhanced benthic CH₄ fluxes. Across seasons, CH₄ production rates and fluxes in seagrass sediments showed relatively stable patterns, indicating that high organic input and plant-mediated conditions help sustain methanogenic processes year-round. Together, these results highlight that seagrass sediments act as consistent CH₄ hotspots due to organic enrichment and microbial processes, while sandy sediments contribute irregular, weather-sensitive CH₄ pulses (Fig. 5b).

It is important to note that benthic chamber incubations can influence fluxes by altering ambient oxygen and microbial dynamics, particularly over longer incubations (Villnas et al., 2012). While in situ incubations are generally regarded as more representative of natural environmental conditions preserving the intact sediment-to-water interface, ambient light, hydrodynamics, and biological interactions (Mallon et al., 2022). However, environmental parameters such as light intensity, temperature, and water chemistry may become more stable or even unintentionally optimized within the chamber, potentially enhancing photosynthetic activity and metabolic rates compared to the more variable and sometimes limiting conditions in the field (Olivé et al., 2016). Moreover, natural water movement, turbidity, and shading from suspended particles can reduce light penetration inside the chamber, thereby limiting photosynthetic efficiency (Mallon et al., 2022).

CH₄ 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, CH₄ production rates and sediment-to-water fluxes were $102.9 \pm 20.2 \mu\text{mol m}^{-3} \text{d}^{-1}$ and $41.2 \pm 8.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in spring, $263.3 \pm 710.4 \mu\text{mol m}^{-3} \text{d}^{-1}$ and $105.3 \pm 284.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in autumn, and $295.0 \pm 35.1 \mu\text{mol m}^{-3} \text{d}^{-1}$ and $118.0 \pm 14.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ in summer, respectively (Table 2). Overall, CH₄ production rates and sediment-to-water fluxes in the seagrass meadow remained relatively stable across seasons (Figure 7b). In contrast, sandy sediments maintained relatively low CH₄ production rates and sediment-to-water fluxes during spring and summer but exhibited a marked increase in autumn (Figure 7b). In spring, the CH₄ production rate was $42.1 \pm 11.1 \mu\text{mol m}^{-3} \text{d}^{-1}$, with a sediment-to-water flux of $16.9 \pm 4.5 \mu\text{mol m}^{-2} \text{d}^{-1}$. In autumn, the CH₄ production rate was substantially higher, reaching $972.2 \pm 957.1 \mu\text{mol m}^{-3} \text{d}^{-1}$, with a sediment-to-water flux of $388.9 \pm 382.8 \mu\text{mol m}^{-2} \text{d}^{-1}$. In summer, the CH₄ production rate was $114.0 \pm 30.6 \mu\text{mol m}^{-3} \text{d}^{-1}$, accompanied by a sediment-to-water flux of $45.6 \pm 12.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ (Table 2).

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3.4 Seasonal porewater CH₄ profiles

In both seagrass and sandy sediments, CH₄ concentrations in the porewater were highest within the upper 0–12 cm, with seagrass sediments consistently exhibiting greater values than sandy sediments (Fig. 6). This pattern reflects enhanced methanogenic activity supported by higher organic content and microbial processes in vegetated sediments. According to the sediment core data, the average total organic carbon content was 0.40%, and it was primarily derived from aquatic plant material and microbial processing (Tang et al., 2025). Beyond 12 cm, CH₄ concentrations in seagrass sediments declined steadily to 20 cm, indicating reduced substrate availability or increased oxidation potential. Such vertical distributions are consistent with previous studies, where sulfate-dependent anaerobic CH₄ oxidation and competition for electron acceptors in anoxic zones have been identified as key drivers (Rissanen et al., 2017). Porewater CH₄ concentrations in seagrass sediments ranged from 6.0–117.0 nM in spring 2022, 6.5–423.2 nM in autumn 2022, and 11.8–364.8 nM in summer 2023 (Fig. 6), broadly corresponding to benthic production rates and fluxes (Table 2). Seasonal variability was evident, with the highest concentrations, production rates, and benthic fluxes in seagrass meadow in autumn and summer (Fig. 5), reflecting enhanced microbial activity and organic matter decomposition.

Seagrass meadows function as carbon sinks by trapping and storing organic matter within sediments (Duarte et al., 2013). Under anaerobic conditions, the decomposition of this organic material promotes methanogenesis, leading to elevated CH₄ production (Dai et al., 2025). Higher concentrations of sediment organic carbon in seagrass beds compared to sandy area have been shown to play a critical role in enhancing CH₄ emissions (Banerjee et al., 2018). These sedimentary conditions, by slowing aerobic microbial decomposition, further favor organic carbon storage and stimulate CH₄ production (Rosentreter et al., 2021a).

CH₄ concentrations in porewater were consistently higher than in overlying water, reflecting diffusion from sediment to water column as a primary transport pathway (Yu et al., 2024). Although sediments are a source of CH₄, a substantial portion may be oxidized in the water column, especially under well-oxygenated conditions (Miller et al., 2017). In seagrass beds, oxygen released during photosynthesis can diffuse into sediments, supporting methanotrophic bacteria that oxidize CH₄ and reducing net emissions. Seagrass roots and rhizospheres may also enhance transportation of oxygen and other reactants, further stimulating CH₄ oxidation (Yau et al., 2023). Additionally, when porewater CH₄ partial pressure exceeded hydrostatic pressure, ebullition occurred, releasing bubbles directly into the water column (Sun et al., 2022). Porewater CH₄ dynamics were further influenced by methanogenesis, oxidation, and organic matter availability (Henriksson et al., 2024; Yau et al., 2023).

Porewater CH₄ concentrations ranged from 9.3–282.0 nM in spring 2022, 9.1–190.3 nM in autumn 2022, and 6.1–256.0 nM in summer 2023 in sandy sediments, and from 6.0–117.0 nM, 6.5–423.2 nM, and 11.8–364.8 nM, respectively, in seagrass sediments (Figure 8), broadly corresponding to the observed benthic CH₄ production rates and sediment-to-water fluxes (Table 2). In seagrass sediments, porewater CH₄ 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 CH₄ 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 CH₄ concentrations than sandy sediments in autumn 2022 and summer 2023, particularly within the upper 12 cm of the sediment column (Figure 8b and 8c). However, this pattern was reversed in spring 2022, when sandy sediments exhibited higher porewater CH₄ concentrations than seagrass sediments below 10 cm depth (Figure 8a). In sandy sediments, porewater CH₄ 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).

3.5 Annual fluxes and implications

The Haikou seagrass meadows and adjacent coastal waters exhibit CH₄ emissions to the atmosphere. The annual sea-to-air flux in seagrass water averaged $4.9 \pm 2.2 \mu\text{mol m}^{-2} \text{d}^{-1}$, higher than the $2.7 \pm 2.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ observed in adjacent coastal waters. This corresponds to an annual CH₄ emission of approximately 78.3 moles from Haikou seagrass water to the atmosphere. Sediment-to-water fluxes were substantially larger, reaching $88.2 \pm 41.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in seagrass meadows and $150.4 \pm 207.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ in sandy areas. Seagrass sediments acted as persistent CH₄ hotspots, sustaining relatively stable emissions even under severe weather conditions, whereas sandy sediments exhibited irregular, weather-driven pulses of CH₄ release. On an annual basis, sandy areas contributed approximately twice the CH₄ flux to the overlying water column compared to seagrass meadows, particularly during severe weather events, although seagrass sediments often exhibited higher baseline emissions than sandy areas. With climate change projected to increase the frequency of extreme weather, benthic CH₄ release from unvegetated sandy areas may intensify. Benthic sediments in the Haikou seagrass meadow released approximately $1,410.1 \text{ mol CH}_4 \text{ yr}^{-1}$ into the overlying seawater, whereas the water column emitted only about $78.3 \text{ mol CH}_4 \text{ yr}^{-1}$ to the atmosphere. The meadow covers an area of approximately 4.38 ha with an average depth of 1 m, and the mean seasonal surface water CH₄ concentration was 8.9 nM, although winter data were unavailable. At this concentration, only 0.39 mol CH₄ was present in the water column at any given time. This imbalance between sediment production and atmospheric emission indicates that roughly 94% of sediment-derived CH₄ was oxidized within the water column before reaching the atmosphere or being transported laterally.

Differences between seagrass and sandy sediments reflect fundamental ecological and microbial contrasts. Seagrass meadows are highly productive ecosystems that contribute large quantities of organic matter, which fuels decomposition and enhances CH₄ production relative to sandy sediment (Yau et al., 2023). Seagrass roots alter sediment conditions by modulating oxygen availability and microbial community composition, thereby influencing the balance between methanogens and methanotrophs (George et al., 2020). Root structures also create conduits that facilitate gas diffusion and ebullition, further mediating CH₄ transport (Li et al., 2021). Consequently, seagrass sediments generally support higher CH₄ concentrations and more regulated fluxes than unvegetated sands (George et al., 2020; Schom et al., 2022). Nevertheless, our findings indicate that unvegetated sediments exhibit irregular, weather-driven pulses of CH₄ release, which may amplify emissions under future climate change scenarios.

In a broader geographic context, CH₄ sea-to-air fluxes from Haikou were comparable to those reported at Koh Mook, Thailand (Halim et al., 2024), and Swan Lake, China (Tan et al., 2025), reflecting similar conditions across Southeast Asian seagrass meadows (Table 3). However, they were substantially lower than fluxes reported in the Chilika Lagoon, India (Banerjee et al., 2019), where tropical seagrass meadows exhibited elevated CH₄ emissions, further amplified by warming conditions and linked to methylophilic methanogenesis (Dai et al., 2025). Caribbean studies also suggest elevated emissions under organic-rich, anoxic conditions, though seasonal variability and plant-mediated oxygenation can moderate fluxes (Saderne et al., 2023). At the global scale, seagrass ecosystems are generally net sources of CH₄ with mean flux of 79.0 $\mu\text{mol m}^{-2} \text{d}^{-1}$ (Eyre et al., 2023), substantially higher than the fluxes observed in our study. According to Eyre et al. (2023), elevated emissions are often reported in lagoons and marshes, where plant-derived methylated compounds stimulate methylophilic methanogenesis.

The sediment-to-water CH₄ fluxes measured in this study fall within a moderate range compared with other investigations (Table 3). Fluxes were similar with those observed in *Enhalus acoroides* in Awerange Bay, Indonesia (Alongi et al., 2000). They were higher than those reported for *Halophila ovalis* and *Zostera muelleri* meadows at Wallis Lake, Australia (Camillini, 2020), but lower than those from South Bay, Virginia (Oreska et al., 2020) and from *Posidonia australis* meadows in Wallis Lake (Camillini, 2020), both of which exhibited substantially greater fluxes. These differences reflect the strong influence of site-specific conditions—sediment organic matter, redox potential, and species traits—on methanogenic activity and gas exchange. Additionally, different seagrass species may contribute differently to CH₄ benthic fluxes (Garcias-Bonet and Duarte, 2017).

Taken together, these findings emphasize the critical importance of region- and species-specific assessments when evaluating seagrass contributions to GHG budgets. Tropical seagrass systems differ fundamentally from temperate analogs in both biogeochemical drivers and microbial processes, and their CH₄ fluxes are further shaped by environmental disturbances, land-use change, and nutrient enrichment (Pajares et al., 2016). To refine global estimates, future research should integrate microbial community profiling, porewater chemistry, isotopic tracing, and trait-based approaches. This is particularly crucial in tropical regions, where CH₄ fluxes can offset a substantial fraction of the climate benefits of blue carbon ecosystems. In Haikou, sea-to-air fluxes remain relatively low, but the elevated benthic fluxes from seagrass sediments and the potential for weather-driven pulses highlight the need for habitat-specific monitoring. Ultimately, these results align with global syntheses (Eyre et al., 2023) showing that CH₄ emissions, while variable, can offset 30–40% of seagrass climate mitigation potential, making it essential to include CH₄ in comprehensive blue carbon assessments.

4. Discussion

4.1 Controls on dissolved CH₄ dynamics and sea-to-air fluxes in a tropical seagrass meadow

Dissolved CH₄ concentrations in the seagrass meadow exhibited pronounced diurnal variability, with surface waters generally peaking at night. This consistent pattern across most sampling periods likely reflects the influence of daytime photosynthesis, which increased DO saturation and may have suppressed CH₄ production or enhanced aerobic CH₄ oxidation, thereby limiting

CH₄ accumulation in the water column. In contrast, lower nighttime DO saturation reduced oxidation potential and allowed sediment-derived CH₄ to accumulate in the shallow water column. The only 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 CH₄ 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 CH₄ dynamics in shallow coastal ecosystems.

Compared with the seagrass meadow, adjacent coastal waters consistently exhibited lower and less variable dissolved CH₄ concentrations. This contrast is likely attributable to the substantially greater water depth (approximately 10 m) at the coastal site, which reduces the influence of sediment-derived CH₄ on surface waters. In contrast, the shallow water depth (0.5–1.5 m) within the seagrass meadow facilitates the transport of benthic CH₄ to the surface, resulting in consistently higher dissolved CH₄ concentrations. Although no significant seasonal differences in surface CH₄ concentrations were observed in either habitat, both the seagrass meadow and adjacent coastal waters acted as net sources of atmospheric CH₄ throughout the study period. Mean sea-to-air CH₄ fluxes were consistently higher in the seagrass meadow ($4.9 \pm 2.2 \mu\text{mol m}^{-2} \text{d}^{-1}$) than in the adjacent coastal waters ($2.7 \pm 2.0 \mu\text{mol m}^{-2} \text{d}^{-1}$; Table 1), indicating that seagrass habitats function as localized CH₄ 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 CH₄ concentrations further suggests that seasonal variability in sea-to-air CH₄ fluxes was primarily governed by changes in wind speed rather than by variations in dissolved CH₄ concentrations, highlighting the dominant role of physical gas transfer in regulating atmospheric CH₄ 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 CH₄ sources. These results emphasize that evaluations of the climate benefits of seagrass ecosystems should consider both their carbon sequestration capacity and their CH₄ emissions, particularly as changes in hydrodynamic conditions and extreme weather events may alter CH₄ exchange between coastal waters and the atmosphere.

4.2 Drivers of seasonal benthic CH₄ production and sediment-to-water fluxes in a tropical seagrass meadow

CH₄ production and benthic fluxes in the seagrass meadow exhibited clear 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 CH₄ production and benthic 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 CH₄ production rates and sediment-to-water fluxes observed during summer and autumn. The seasonal increase in benthic CH₄ production is supported by the porewater CH₄ profiles, which showed markedly 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 CH₄ concentrations observed during the warmer seasons. Similar relationships between sediment organic carbon and CH₄ production have been reported in other seagrass ecosystems, where the decomposition of seagrass detritus enhances microbial activity and promotes methanogenesis (Dai et al., 2025; Dai et al., 2026; Schorn et al., 2022). Dense seagrass canopies also reduce sediment oxygen penetration and create anoxic conditions favorable for methanogenic archaea, resulting in greater CH₄ production than in adjacent unvegetated sandy sediments (Saderne et al., 2023; Sogin et al., 2022). Furthermore, the ability of seagrass meadows to trap and retain organic matter enhances long-term carbon storage while simultaneously providing substrates that can support CH₄ production under anaerobic conditions (Banerjee et al., 2018; Duarte et al., 2013; Rosentreter et al., 2021a).

Porewater CH₄ concentrations were consistently higher than those in the overlying water, indicating that sediment diffusion represented the primary pathway supplying CH₄ to the water column (Yu et al., 2024). However, only a fraction of the CH₄ produced in sediments is ultimately emitted to the atmosphere because substantial oxidation can occur before reaching the water surface. During daytime, oxygen released by seagrass photosynthesis diffuses into sediments and the rhizosphere, stimulating methanotrophic bacteria that consume CH₄ and thereby reduce net emissions (Miller et al., 2017; Yau et al., 2023). In addition, the decline in porewater CH₄ concentrations with sediment depth observed in this study is consistent with previous findings that sulfate-dependent anaerobic oxidation of methane and competition for electron acceptors can limit CH₄ 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 CH₄ release when porewater CH₄ partial pressure exceeds hydrostatic pressure, allowing CH₄ bubbles to bypass oxidation within the sediment and water column (Sun et al., 2022). Therefore, the observed porewater CH₄ distributions likely reflect a dynamic balance among organic matter availability, microbial methanogenesis, aerobic and anaerobic CH₄ 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 CH₄ 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 CH₄ production, and sediment-to-water transport explains the elevated benthic CH₄ fluxes observed during summer and autumn, while subsequent oxidation within the sediment and water column moderates the fraction of CH₄ ultimately released to the atmosphere.

4.3 Contrasting benthic CH₄ dynamics between seagrass and sandy sediments

In situ benthic chamber incubations demonstrated clear differences in CH₄ dynamics between seagrass and adjacent sandy sediments. During both daytime and nighttime in spring 2022 and summer 2023, CH₄ production rates and sediment-to-water fluxes were consistently higher in seagrass sediments than in adjacent sandy 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 CH₄ 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 CH₄ to diffuse or escape into the overlying water column, thereby enhancing CH₄ emissions from seagrass habitats (Li et al., 2021; Yau et al., 2023). Collectively, these biological and biogeochemical processes explain why seagrass sediments generally support higher CH₄ production and more sustained sediment-to-water fluxes than adjacent sandy sediments (George et al., 2020; Schorn et al., 2022).

An exception to this general pattern occurred during the autumn 2022 sampling, when daytime CH₄ production rates and benthic fluxes in sandy 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 CH₄. 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 CH₄ pulses despite their generally higher background CH₄ production. These contrasting responses were also reflected in the seasonal averages. Mean sediment-to-water CH₄ fluxes were $88.2 \pm 41.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the seagrass meadow and $150.4 \pm 207.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ in the adjacent sandy sediments (Table 2). However, the higher seasonal mean for sandy sediments was largely driven by the exceptionally high emissions recorded during the storm-affected autumn sampling. Excluding this episodic event, seagrass sediments consistently exhibited higher baseline CH₄ production and benthic fluxes, whereas sandy sediments generally maintained much lower emissions. These findings indicate that seagrass sediments function as persistent CH₄ sources sustained by continuous organic matter decomposition and microbial methanogenesis, whereas unvegetated sandy sediments are characterized by relatively low background emissions punctuated by irregular, disturbance-driven CH₄ pulses. As climate change is projected to increase the intensity and frequency of typhoons and other extreme weather events (IPCC, 2021), episodic CH₄ release from sandy coastal sediments may become an

increasingly important component of coastal GHG budgets, even though seagrass meadows remain the dominant long-term hotspots for benthic CH₄ production.

4.4 The fate of sediment-derived CH₄ in a tropical seagrass meadow

Despite acting as a net atmospheric CH₄ source, sediment-to-water CH₄ 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 CH₄ production and atmospheric emissions. A simple mass-balance comparison further demonstrates that only a small fraction of sediment-derived CH₄ 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, 415, and 465 mol CH₄ into the overlying water column during spring, autumn, and summer, respectively. In comparison, only 21, 27, and 10 mol CH₄ were emitted to the atmosphere during the corresponding sampling periods. Consequently, approximately 87% of sediment-derived CH₄ in spring, 94% in autumn, and 98% in summer did not reach the atmosphere directly. Instead, much of this CH₄ 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 CH₄ in the water column (0.33–0.43 mol across seasons), despite substantial benthic inputs, further supports the rapid turnover and efficient redistribution of CH₄ within this shallow, hydrodynamically active seagrass ecosystem.

These findings demonstrate that benthic CH₄ production cannot be directly translated into atmospheric emissions. Rather, the fate of sediment-derived CH₄ 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 CH₄ 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 CH₄ 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 CH₄ from the meadow before atmospheric emission. Future studies integrating hydrodynamic observations, direct measurements of CH₄ oxidation rates, and continuous

flux measurements across tidal cycles will help better constrain the fate of sediment-derived CH₄ and improve GHG budgets for blue carbon ecosystems.

4.5 Regional and Global Context of CH₄ Fluxes in Seagrass Ecosystems

In a broader geographic context, the sea-to-air CH₄ 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 CH₄ 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 CH₄ emissions that were further enhanced under warming conditions through methylotrophic methanogenesis (Dai et al., 2025). Likewise, studies from the Caribbean have reported elevated CH₄ 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 CH₄ 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 CH₄ emissions are typically associated with lagoons and salt marshes, where abundant plant-derived methylated compounds promote methylotrophic methanogenesis.

The sediment-to-water CH₄ 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 CH₄ transport. In addition, species-specific traits, such as belowground biomass, root oxygen release, and organic matter inputs, are likely to contribute to differences in benthic CH₄ 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 CH₄ production and emissions (Pajares et al., 2016). Future studies should integrate microbial community analyses, porewater geochemistry, isotopic tracers, and trait-based approaches to better resolve the mechanisms controlling CH₄ cycling across different seagrass ecosystems. Such efforts are particularly important in tropical regions, where CH₄ emissions have the potential to offset a substantial proportion of the climate mitigation benefits associated with blue carbon storage. Although the sea-to-air CH₄ fluxes measured at Haikou were relatively low compared with the global average, the consistently elevated benthic CH₄ production within the seagrass meadow and the potential for episodic, weather-driven CH₄ 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 CH₄ emissions can partially offset the climate mitigation benefits of seagrass ecosystems and therefore should be incorporated into comprehensive blue carbon assessments.

4.5. Conclusions

This study ~~provides~~^{presents} the first integrated assessment of seasonal and ~~annual-diurnal~~ CH₄ dynamics linking sediment production, sediment-to-water fluxes, and sea-to-air emissions in a tropical *Thalassia hemprichii* and *Halophila pinifolia* seagrass meadow in Haikou, Taiwan. ~~in Taiwan's seagrass ecosystems, focusing on the Haikou meadows and adjacent coastal waters. By combining surface water observations, sea-to-air fluxes, benthic incubations, and porewater profiles, we reveal the interplay between biogeochemical processes, sediment conditions, and environmental drivers that regulate CH₄ production and emissions in tropical seagrass coasts. Seagrass waters consistently showed higher CH₄ concentrations than nearby coastal waters, reflecting shallow depths and stronger sedimentary influence. Sea-to-air fluxes confirmed that seagrass habitats are CH₄ hotspots, with autumn 2022 peaks under strong winds. Sediment incubations indicated benthic dominance of CH₄ production, with seagrass sediments maintaining stable rates across seasons, while sandy sediments exhibited episodic storm-driven peaks that highlight the potential for extreme weather to amplify emissions. Porewater profiles showed elevated CH₄ in the upper 0–12 cm of seagrass sediments, declining with depth due to substrate limitation and anaerobic oxidation, while higher porewater than water column concentrations confirmed diffusion as key pathway. Oxygen release from seagrass roots likely stimulated methanotrophy, partially offsetting production. Annual sea-to-air fluxes averaged $4.9 \pm 2.2 \mu\text{mol m}^{-2} \text{d}^{-1}$ in seagrass waters compared with $2.7 \pm 2.0 \mu\text{mol m}^{-2} \text{d}^{-1}$ in coastal waters, equivalent to approximately 78.3 moles CH₄ emission to the atmosphere per year. Although sediment-to-water fluxes were substantial, about 94% of CH₄ was oxidized before reaching the atmosphere or being transported laterally. Overall, seagrass meadows act as both carbon sinks and CH₄ sources, with their net climate effect depending on the balance between long-term carbon burial and CH₄ release. Compared with global averages, CH₄ fluxes in Haikou are moderate but ecologically significant, given the widespread extent of seagrass meadows in Southeast Asia and the limited data available for tropical seagrass ecosystems in Taiwan. In contrast to episodic pulses from unvegetated sands, seagrass meadows may buffer against climate variability. Incorporating CH₄ dynamics into blue carbon strategies is therefore essential, requiring accounting frameworks that consider both sequestration and emissions to evaluate the true climate mitigation potential of seagrass ecosystems. The seagrass meadow consistently exhibited higher dissolved CH₄ concentrations and sea-to-air CH₄ fluxes than adjacent coastal waters, confirming that it functions as a localized atmospheric CH₄ hotspot. Seasonal variability in atmospheric CH₄ emissions was primarily controlled by wind-driven gas exchange rather than changes in dissolved CH₄ concentrations, while benthic CH₄ production and sediment-to-water fluxes were strongly influenced by seasonal hydrodynamic conditions that regulated organic matter accumulation and microbial methanogenesis. Compared with adjacent sandy sediments, seagrass sediments maintained consistently higher baseline CH₄ production and~~

benthic fluxes owing to greater organic matter availability and favorable microbial conditions, although storm-induced sediment disturbance generated episodic CH₄ release from unvegetated sandy sediments.

620 Despite substantial benthic CH₄ production, only a small proportion of sediment-derived CH₄ was emitted directly to the atmosphere, indicating a pronounced decoupling between sediment production and atmospheric emissions. The majority of CH₄ 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 CH₄ fluxes measured at Haikou were lower than the global average for seagrass ecosystems, the benthic CH₄ fluxes fell within the range reported

625 worldwide, emphasizing the importance of local environmental conditions and species-specific characteristics in regulating CH₄ 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, CH₄ oxidation rates, and continuous observations across tidal and seasonal cycles will improve our understanding of the fate of sediment-derived CH₄ and reduce uncertainties in blue carbon GHG budgets under future

630 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.

635

Competing interests

640 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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Table 1. Diurnal and seasonal variations in marine environmental conditions, CH₄ concentrations, and sea-to-air fluxes.

Season	Area	Time	T (°C)	S	DO%	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	5.4 ± 3.0
		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			
	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			
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	6.8 ± 3.1
		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			
	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			
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	2.5 ± 0.8
		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			
	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			
Annual	Seagrass Water								4.9 ± 2.2
	Coastal Water								2.7 ± 2.0

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Table 2. Seasonal variations in-situ benthic chamber incubations of CH₄ production rates and sediment-to-water fluxes.

Season	Sampling date	Habitat	Production Rates			Sediment-to-water flux		
			day (μ mole m ⁻³ h ⁻¹)	night (μ mole m ⁻³ h ⁻¹)	seasonal (μ mole m ⁻³ d ⁻¹)	day (μ mole m ⁻² h ⁻¹)	night (μ mole m ⁻² h ⁻¹)	seasonal (μ mole 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
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
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
Annual		seagrass			220.4 ± 103.0			88.2 ± 41.2
		sand			376.1 ± 517.5			150.4 ± 207.0

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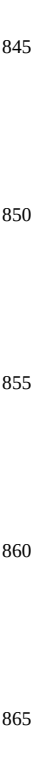
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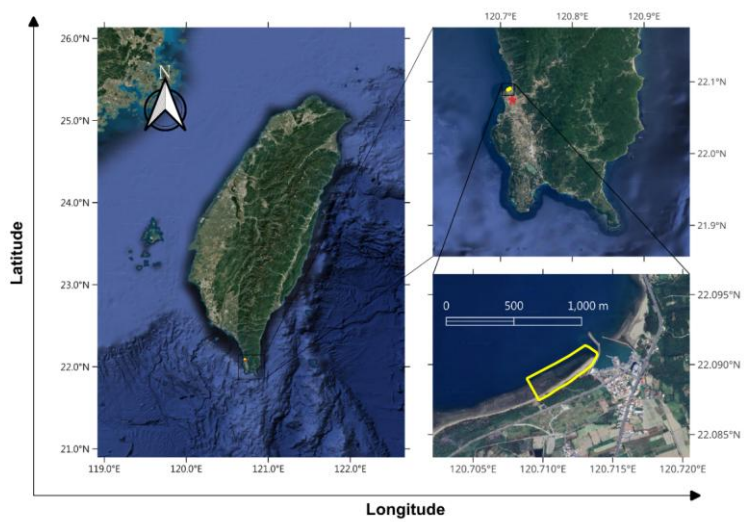
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840 Table 3. The global CH₄ sea-to-air and sediment-to-water fluxes

Location	Species	Site	Climate	Water Depth (m)	Method	Sea-to-air Flux (μmol m ⁻² d ⁻¹)	Method	Sediment-to-water Flux (μmol m ⁻² d ⁻¹)	References
Wallagoot, Australia	<i>Ruppia megacarpa</i>	Mouth of estuary	Temperate	0.8	Continuous surface water	33.8			
	<i>Halophila ovalis</i>			1.7				45.4	(Caimillini, 2020)
Wallis Lake, Australia	<i>Posidonia australis</i>	Mouth of estuary	Temperate	1.2			Benthic chamber	279.3	
	<i>Zostera muelleri</i>			0.9				46.0	
Swan Bay, Australia	<i>Zostera muelleri</i>	Tidal lagoon	Temperate	-	Continuous surface water	10.5			(Olivé et al., 2016)
South Bay, Virginia, USA	<i>Zostera marina</i>	Coastal bay with marsh	Temperate	-			Benthic chamber	136.7 ± 127.8	(Oreska et al., 2020)
East Harbor, Massachusetts, USA	<i>Zostera marina</i>	Lagoon-marsh	Temperate	1	Discrete water samples	107.5	Benthic chamber	0.0	
Pleasant Bay, Massachusetts, USA	<i>Zostera marina</i>	Coastal lagoon	Temperate	2		113.8		73.3	(Al-Haj et al., 2022)
Cadaques, Spain	<i>Posidonia oceanica</i>	Coastal bay	Temperate	2-10	Continuous surface	0.1 ± 0.1	Porewater samples	0.3 ± 0.1	(Yau et al., 2023)
Ria Formosa Lagoon, Portugal	<i>Zostera noltii</i>	Coastal lagoon	Temperate	Intertidal zones	Dynamic flux chamber	307.2			(Bahlmann et al., 2015)
Baltic Sea, Finland	<i>Zostera marina</i>	Coastal bay	Temperate	2				1.6 ± 1.6	
Kattegat, Denmark	<i>Zostera marina</i>	Fjord-coastal Bay	Temperate	2			Benthic chamber	3.4 ± 0.5	(Asplund et al., 2022)
Skagerrak, Sweden	<i>Zostera marina</i>	Coastal bay	Temperate	2.2				2.5 ± 2.8	
Mediterranean Sea, Italy	<i>Posidonia oceanica</i>	Coastal bay	Temperate	NA			Porewater	106.0	(Schom et al., 2022)
Swan lake, Shandong, China	<i>Zostera marina</i> , <i>Zostera japonica</i>	Coastal lagoon	Temperate	0.5-1.5	Water samples	5.5 ± 8.4			(Fan et al., 2025)
	<i>Enhalus acoroides</i>			Shallow shelves				96.2	
	<i>Thalassodendron ciliatum</i>							3.2	
	<i>Halophila decipiens</i>							1.4	
Red Sea, Saudi Arabia	<i>Thalassia hemprichii</i>	Coastal inlet	Tropical				Core incubation	6.5	(Garcias-Bonet and Duarte, 2012)
	<i>Halophila</i> , <i>Halodule</i> spp.							61.0	
	<i>Halodule uninervis</i>							48.1	
	<i>Cymodocea serrulata</i> , <i>Halodule uninervis</i>							401.3	
Chilika Lagoon, India	<i>Halodule</i> sp., <i>Halophila</i> sp.	Tidal lagoon	Tropical	0.9-2.6	Discrete water samples	120.0			(Banerjee et al., 2018)
Average Bay, Indonesia	<i>Enhalus acoroides</i>	Coastal bay	Tropical	14			Sediment core	95.7 ± 95.4	(Alongi et al., 2008)
Koh Moek, Thailand	<i>Enhalus acoroides</i>	Coastal inlet	Tropical	Intertidal zones	Benthic chamber	3.1			(Halim et al., 2024)
	<i>Thalassia hemprichii</i>					2.0			
Haikou, Taiwan	<i>Thalassia hemprichii</i> , <i>Halodule pinifolia</i>	Coastal inlet	Tropical	0.5-1.5	Discrete water samples	4.9 ± 2.2	Benthic chamber	88.2 ± 41.2	This study





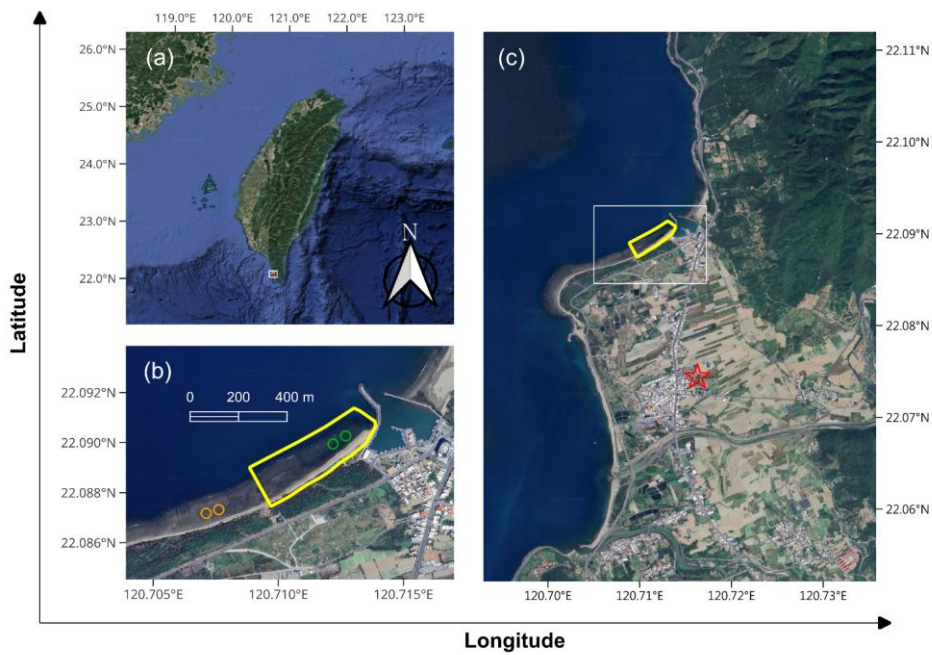


Figure 1. Study area. (The yellow rectangle indicates the seagrass meadow area, while the red star marks the Checheng Weather Station.) (a) Regional map showing the location of the study area. (b) Close-up view of the benthic chamber incubation sites. The yellow rectangle outlines the Haikou seagrass meadow. (c) Zoomed-in map of the study area. The red star indicates the location of the Checheng Weather Station.

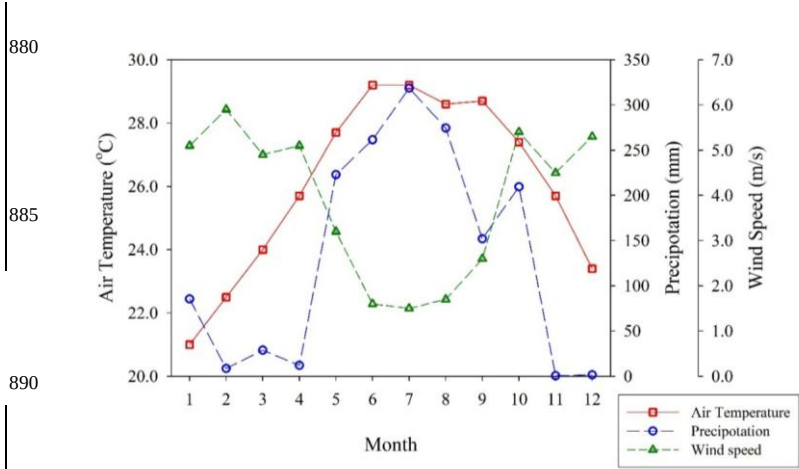


Figure 2. Monthly mean air temperature, total precipitation, and mean wind speed recorded at the Checheng Weather Station during 2022-2023.

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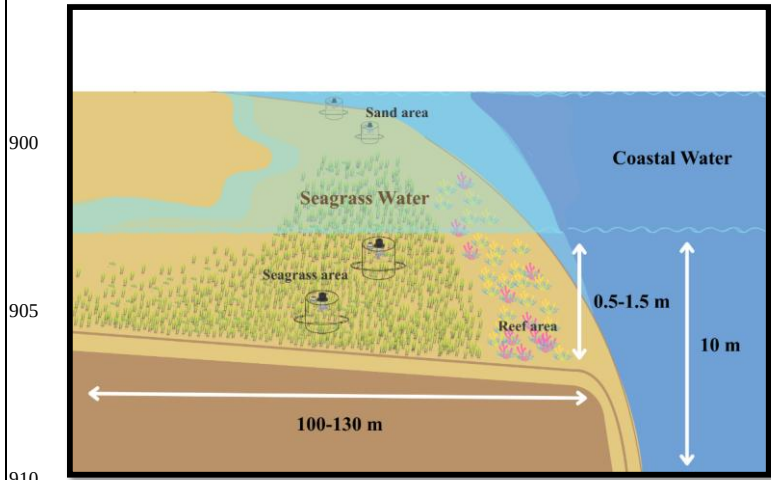


Figure 3. Conceptual diagram illustrating the geographic setting of the study area, including the seagrass meadow, adjacent sandy area, reef platform, and coastal water site.

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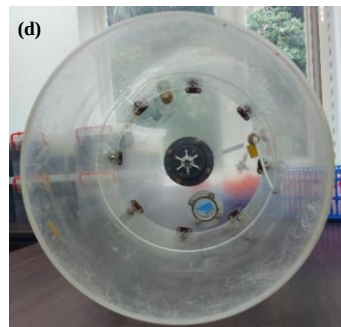
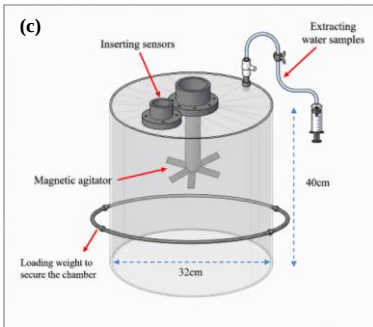


Figure 24. In situ benthic chamber incubation system deployed in (a) the seagrass meadow and (b) adjacent bare sediment, with (c) a schematic illustration of the chamber design and (d) an upward view from inside the chamber.

~~Benthic chamber in situ incubation systems deployed in (a) seagrass and (b) bare sediment environments, with (c) schematic diagram illustrating the chamber design.~~

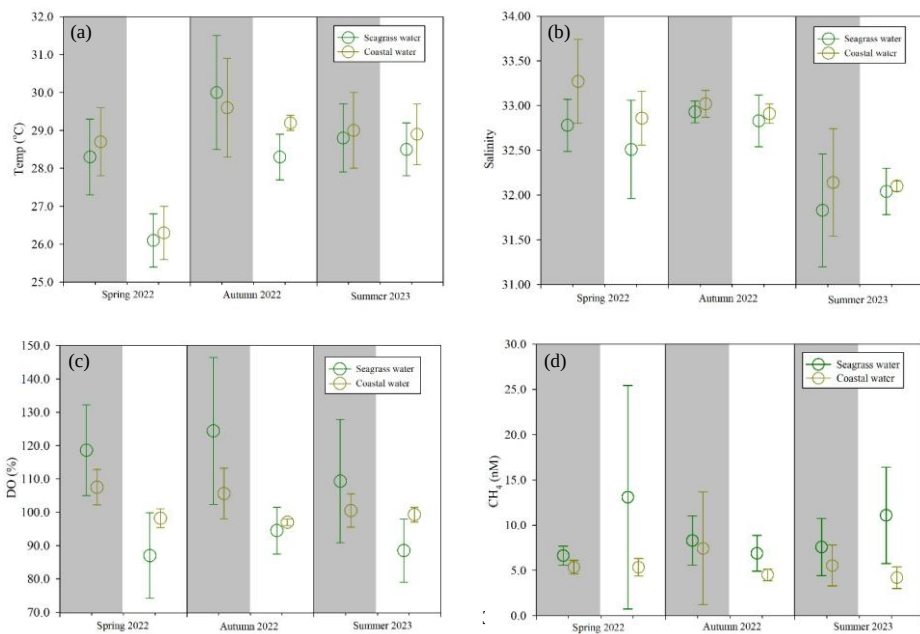
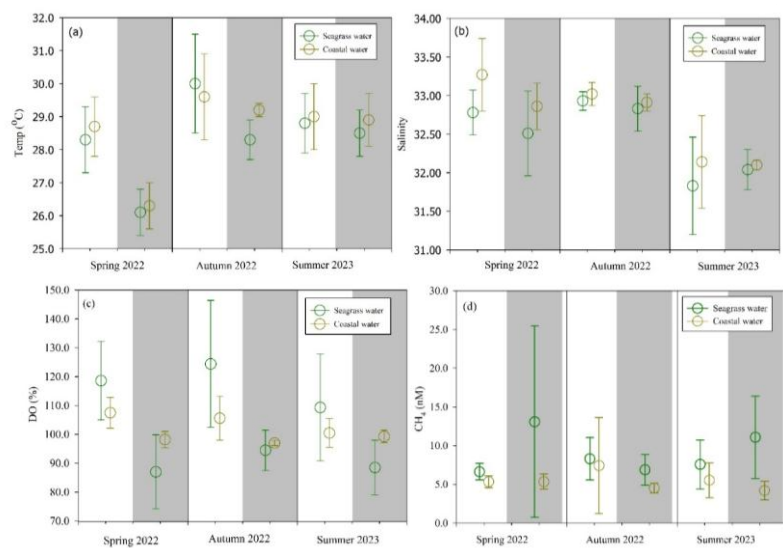


Figure 35. Seasonal environmental conditions of (a) temperature, (b) salinity, (c) DO%, and (d) CH₄ concentrations in seagrass water and coastal water. Bright areas indicate daytime, and grey areas indicate nighttime.

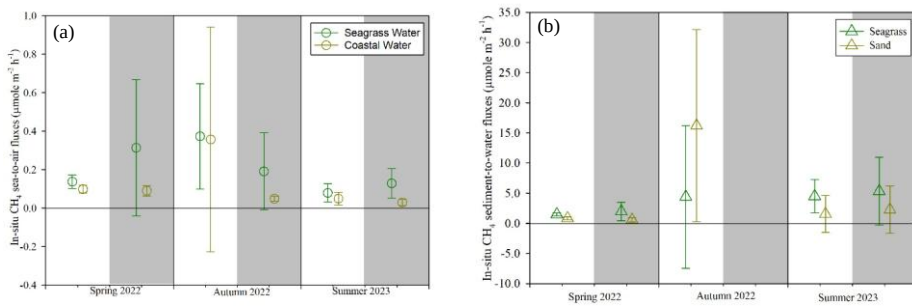
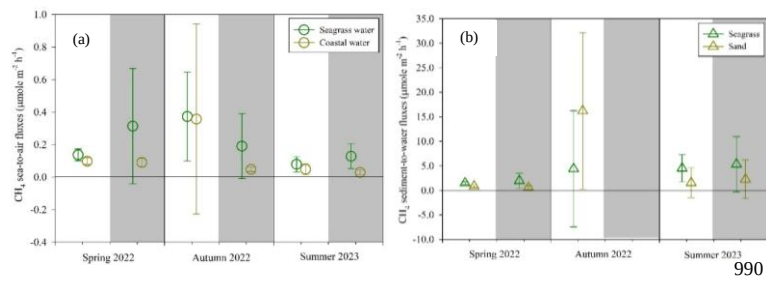


Figure 46. Diurnal variation of CH₄ (a) sea-to-air fluxes (μmole m⁻² h⁻¹; n=226) and (b) sediment-to-water fluxes (μmole m⁻² h⁻¹; n=284) in seagrass water and coastal water. Bright areas indicate daytime, and grey areas indicate nighttime.

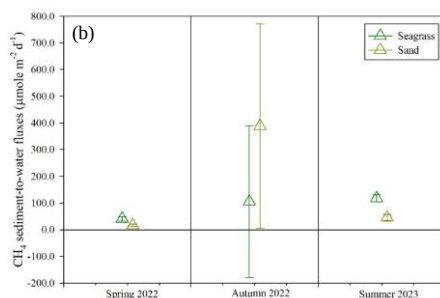
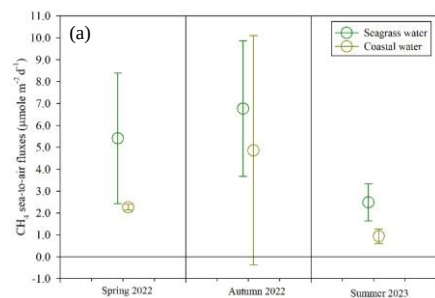
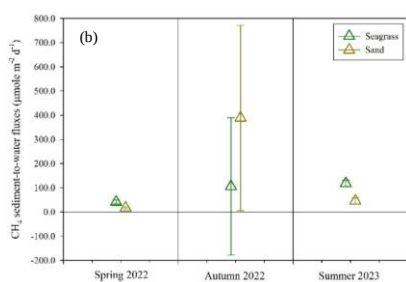
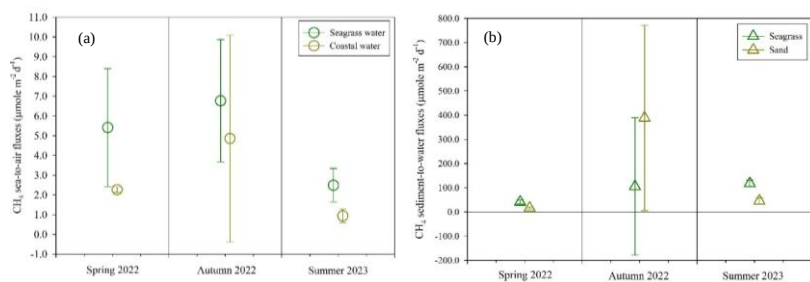


Figure 57. Seasonal variation of CH_4 (a) sea-to-air fluxes ($\mu\text{mole m}^{-2} \text{d}^{-1}$; $n=226$) and (b) sediment-to-water fluxes ($\mu\text{mole m}^{-2} \text{d}^{-1}$; $n=284$) in seagrass water and coastal water.

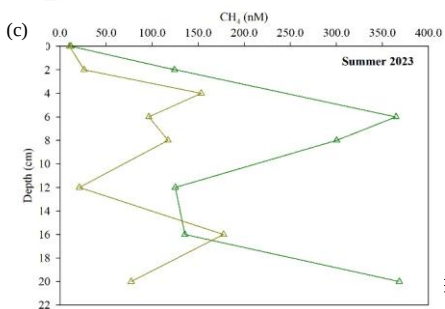
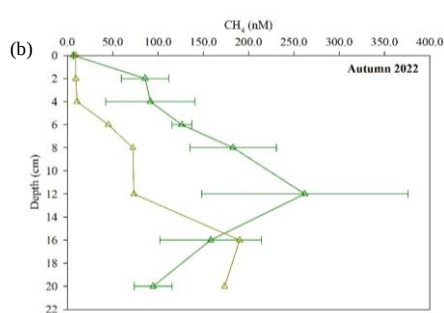
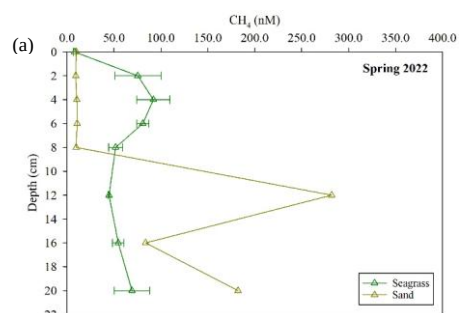
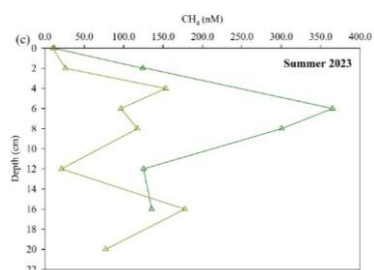
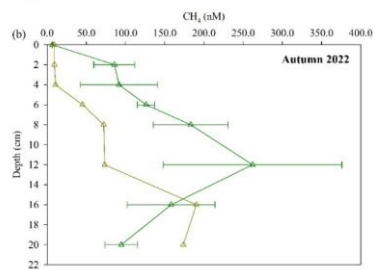
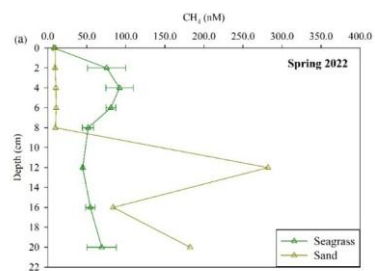


Figure 68. CH_4 concentration profiles in porewater: (a) spring 2022 (n=32), (b) autumn 2022 (n=32), and (c) summer 2023 (n=15). Error bars represent the range of duplicate samples; error bars are absent for depth intervals where only single sample was available. CH_4 concentration profiles in porewater: (a) spring 2022 (n=32), (b) autumn 2022 (n=32), and (c) summer 2023 (n=15).

Vertical line on the left margin.

