

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 (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, 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., 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.

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 Magonigal, 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., 2021b; 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 $\text{CH}_4 \text{ yr}^{-1}$ 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 CH₄ emissions, studies of CH₄ cycling in tropical seagrass ecosystems remain scarce. This study provides the first comprehensive assessment of CH₄ 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 CH₄ production and fluxes in both seagrass and adjacent bare sandy sediments across the sediment-to-water and water-to-air interfaces. This integrated approach provides new insights into the temporal variability and environmental controls of CH₄ 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*—*Halophila pinifolia* (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.

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 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 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.

100 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. All experiments were performed in duplicate.

105 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. To ensure continuous water circulation, a magnetic agitator was positioned inside the chamber (Figure 4d). Water samples were collected using a three-way valve installed on the incubator, while temperature, salinity, and dissolved
110 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.

Water samples for CH₄ 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 (HgCl₂) to inhibit microbial
115 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). Samples 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, and stored at 4 °C in dark until analysis.

120 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, 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
125 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).

2.3 The CH₄ saturation ratio and water-air fluxes

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

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

130 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 (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 et al., 2026).

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

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

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

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

Here, Sc is the Schmidt number for CH₄, and u represents wind speed (m/s). Monthly wind speed data were obtained from the

140 Checheng Weather Station (120.7162°E, 22.0744°N), operated by Taiwan's Central Weather Administration.

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 depending on wave and weather conditions. We estimated the benthic production rates and fluxes of sediment water-interface in in-situ incubation with this following formula:

$$145 \text{ Production rate} = \left(\frac{\Delta C}{\Delta t}\right) \quad (4)$$

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

where $F_{\text{sediment-water}}$ is sediment–water flux ($\mu\text{mol m}^{-2} \text{ h}^{-1}$ or $\mu\text{mol m}^{-2} \text{ d}^{-1}$); 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 (m^3); A_{chamber} is the area of the chamber (m^2).

150 3. Results

3.1 Seasonal and diurnal variability in surface water conditions

Surface water temperatures ranged from 24.6 to 32.0 °C. 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
155 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 fluxes

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 CH₄ dynamics and sediment-to-water fluxes

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 CH_4 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).

3.4 Seasonal porewater CH_4 profiles

190 Porewater CH_4 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 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, 195 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 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 CH_4 concentrations than seagrass sediments below 10 cm depth 200 (Figure 8a). In sandy 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

205 Dissolved CH_4 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 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. The only exception occurred during autumn 2022, when 210 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.

215 Compared with the seagrass meadow, adjacent coastal waters consistently exhibited lower and less variable dissolved CH_4 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 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 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 (Schorn et al., 2022; Dai et al., 2026; Dai et al., 2025). 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 (Duarte et al., 2013; Banerjee et al., 2018; Rosentreter et al., 2021a).

255 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).
260 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
265 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
270 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
275 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
280 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 (Yau et al., 2023; Li et al., 2021). 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 mole CH₄ into the overlying water column during spring, autumn, and summer, respectively. In comparison, only 21, 27, and 10 mole 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 mole 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.

5. Conclusions

This study provides the first integrated assessment of seasonal and 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. 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.

385 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
390 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
395 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,
400 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

405 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.
- 420 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.
- 425 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
430 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
435 Seagrasses Through Methylophilic Methanogenesis, *Geophysical Research Letters*, 52, e2024GL113824, <https://doi.org/10.1029/2024GL113824>, 2025.

- Dai, G., Chen, X., Zhuang, G., Zhu, P., Sun, Y., Wang, Q., Ju, F., Sun, Y., and Li, L.: Porewater-Surface Water Interface Mediates Methanogenesis, Oxidation, and Large Methane Emissions in Mixed Seagrass-Macroalgae Ecosystems, *Journal of Geophysical Research: Oceans*, 131, 10.1029/2025jc023733, 2026.
- 440 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-
445 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*
450 *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,
455 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*
460 *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*
465 *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.

- 470 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.
- 475 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 *Methylo Marinum* in seagrass ecosystem, *Environmental Microbiome*, 20, 67, 10.1186/s40793-025-00736-z, 2025.
- Lin, H. J., Chen, K. Y., Kao, Y. C., Lin, W. J., Lin, C. W., and Ho, C. W.: Assessing Coastal Blue Carbon Sinks in Taiwan, *Marine Research*, 3(2), 10.29677/MR.202312_3(2).0001, 2023.
- 480 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.
- 485 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.
- 490 Miller, C. M., Dickens, G. R., Jakobsson, M., Johansson, C., Koshurnikov, A., and Regan, M., Muschitiello, F., Stranne, C., and Mörtz, C.-M.: Pore water geochemistry along continental slopes north of the East Siberian Sea: inference of low methane concentrations, *Biogeosciences*, 14, 2929-2953, 10.5194/bg-14-2929-2017, 2017.
- 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.
- 495 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.
- 500 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, 2016.
- Reeburgh, W. S.: Oceanic Methane Biogeochemistry, *Chemical Reviews*, 107, 486-513, 2007.

- Rissanen, A. J., Karvinen, A., Nykanen, H., Peura, S., Tirola, 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., Al-Haj, A. N., Fulweiler, R. W., and Williamson, P.: Methane and Nitrous Oxide Emissions Complicate Coastal Blue Carbon Assessments, *Global Biogeochemical Cycles*, 35, 10.1029/2020gb006858, 2021a.
- 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, 2021b.
- Roth, F., Wild, C., Carvalho, S., Rådecker, 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 Ionization 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 Data*, 24, 356-360, 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, 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	
		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	
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	
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	
Seasonal Average	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	night	seasonal	day	night	seasonal
			($\mu\text{mole m}^{-3} \text{ h}^{-1}$)		($\mu\text{mole m}^{-3} \text{ d}^{-1}$)	($\mu\text{mole m}^{-2} \text{ h}^{-1}$)		($\mu\text{mole m}^{-2} \text{ d}^{-1}$)
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
Seasonal Average		seagrass	220.4 ± 103.0			88.2 ± 41.2		
		sand	376.1 ± 517.5			150.4 ± 207.0		

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605 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	(Camillini, 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	(Al-Haj et al., 2022)
Pleasant Bay, Massachusetts, USA	<i>Zostera marina</i>	Coastal lagoon	Temperate	2		113.8		73.3	
Cadaques, Spain	<i>Posidonia oceanica</i>	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	<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	(Schorn 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			(Tan et al., 2025)
	<i>Enhalus acoroides</i>							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	Shallow shelves			Core incubation	6.5	(Garcias-Bonet and Duarte, 2017)
	<i>Halophila</i> , <i>Halodule</i> spp.							61.0	
	<i>Halodule uninervis</i>							48.1	
	<i>Cymodocea serrulate</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)
Awerange Bay, Indonesia	<i>Enhalus acoroides</i>	Coastal bay	Tropical	14			Sediment core	95.7 ± 95.4	(Alongi et al., 2008)
Koh Mook, 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

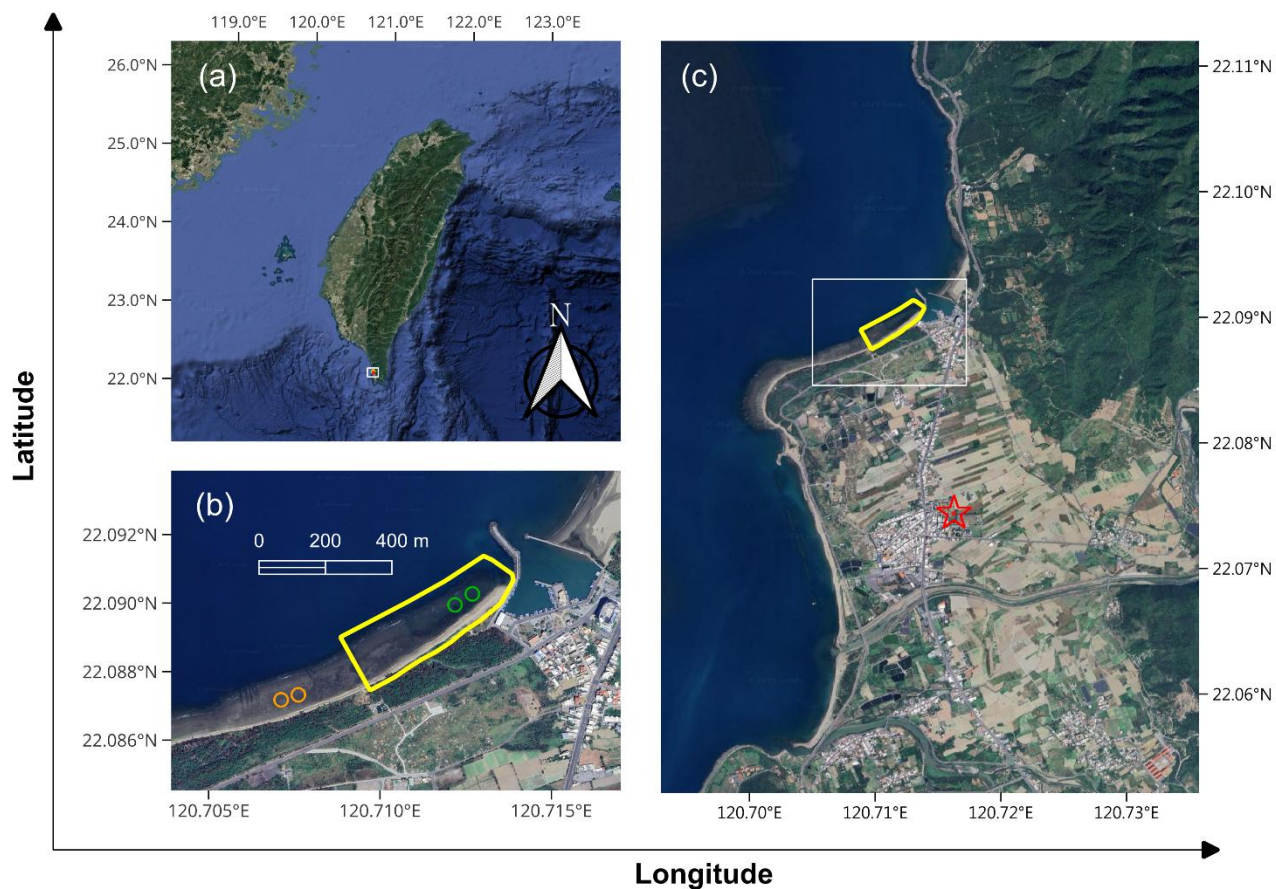


Figure 1. Study area. (a) Regional map showing the location of the study area. (b) Close-up view of the benthic chamber incubation sites. The yellow rectangle outlines the Haikou seagrass meadow. (c) Zoomed-in map of the study area. The red star indicates the location of the Checheng Weather Station.

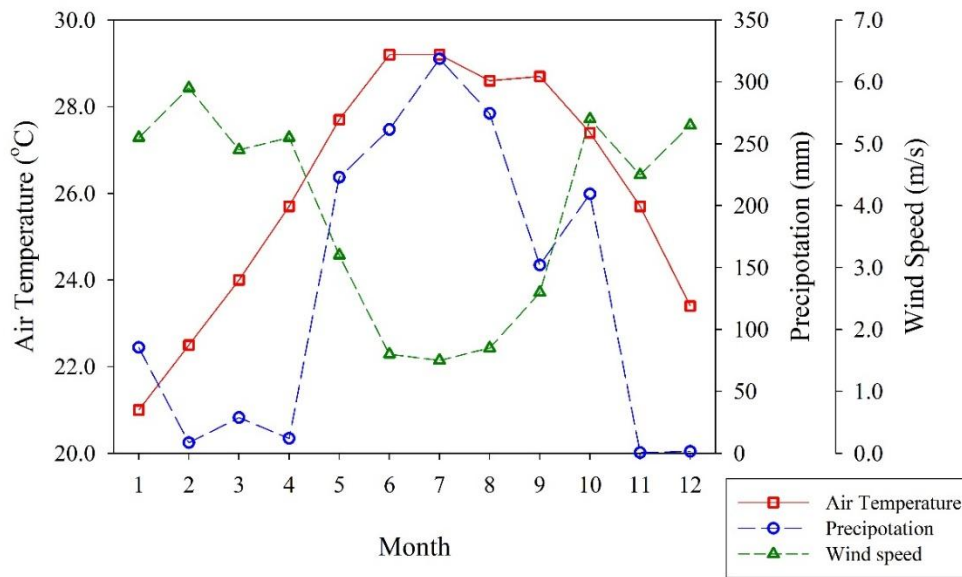


Figure 2. Monthly mean air temperature, total precipitation, and mean wind speed recorded at the Checheng Weather Station during 2022–2023.

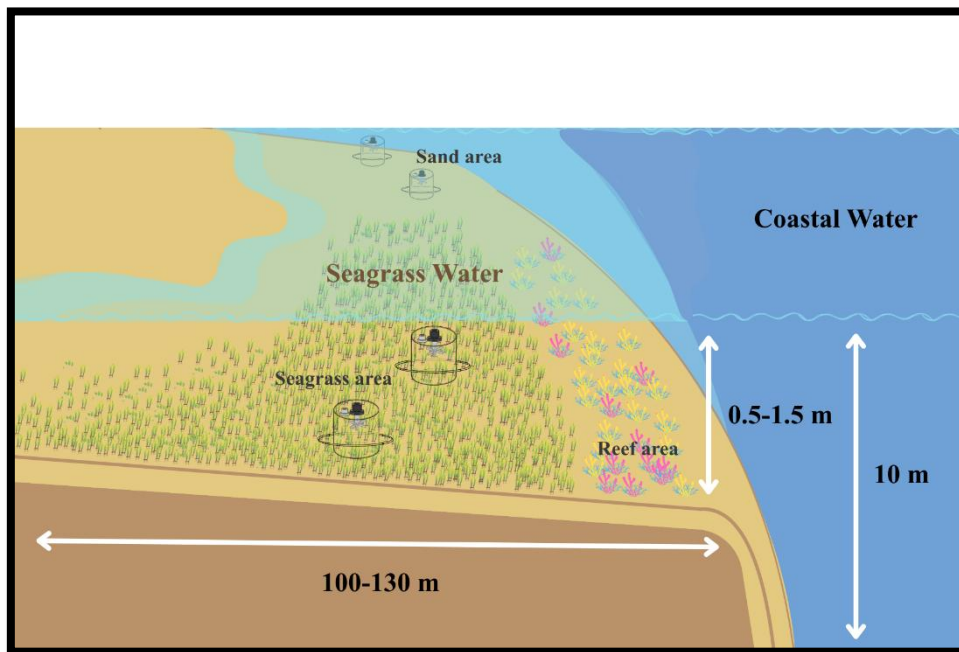


Figure 3. Conceptual diagram illustrating the geographic setting of the study area, including the seagrass meadow, adjacent sandy area, reef platform, and coastal water site.

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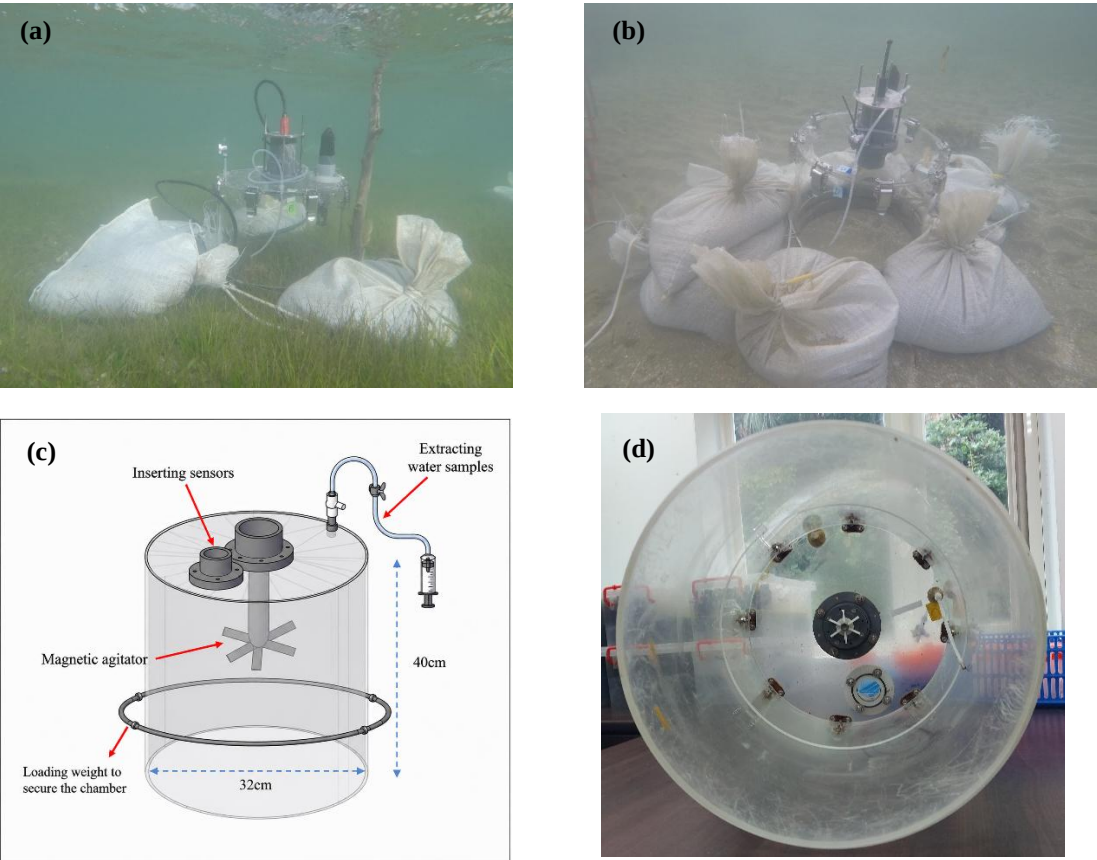
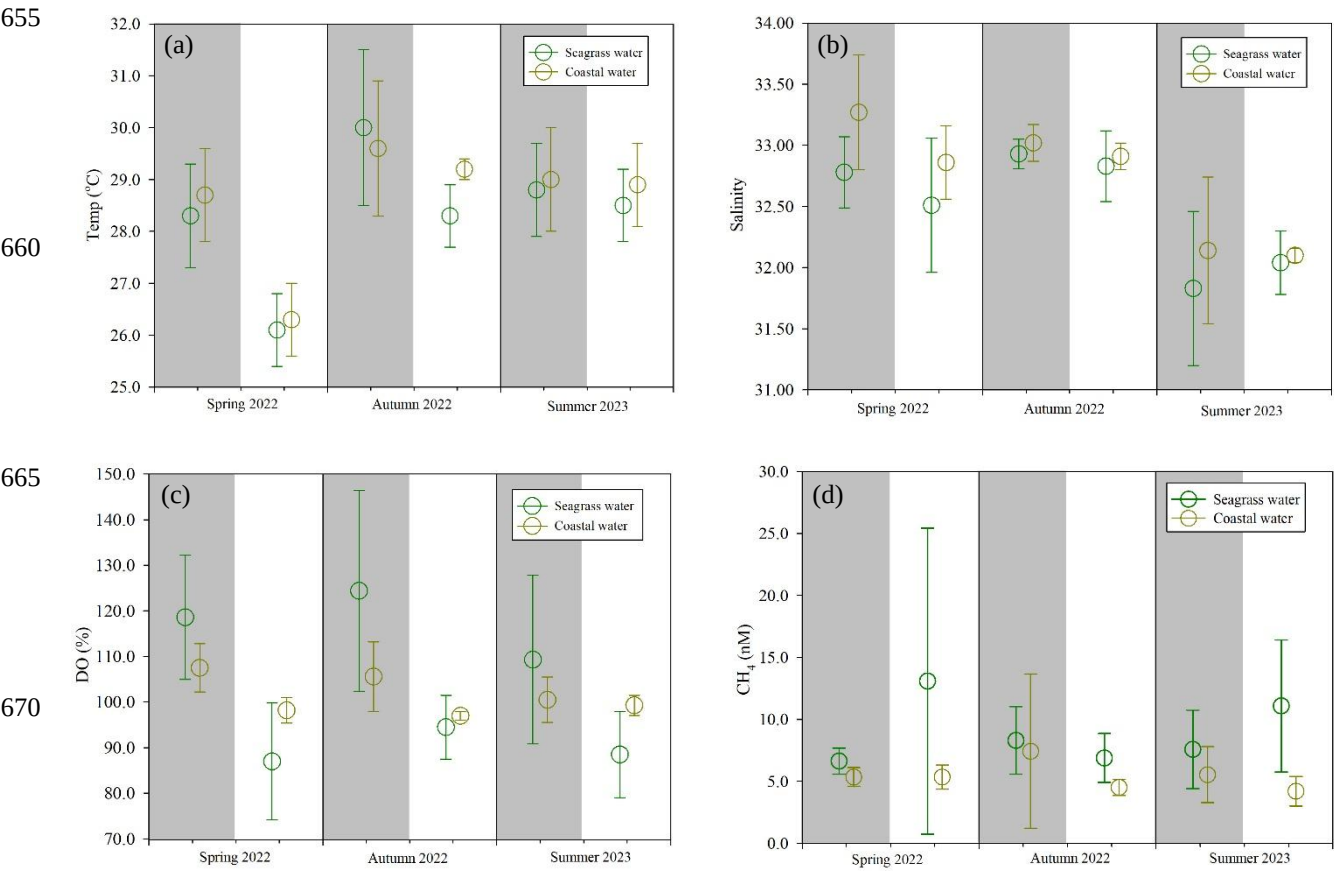


Figure 4. In situ benthic chamber incubation system deployed in (a) the seagrass meadow and (b) adjacent bare sediment, with (c) a schematic illustration of the chamber design and (d) an upward view from inside the chamber.



675 Figure 5. 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.

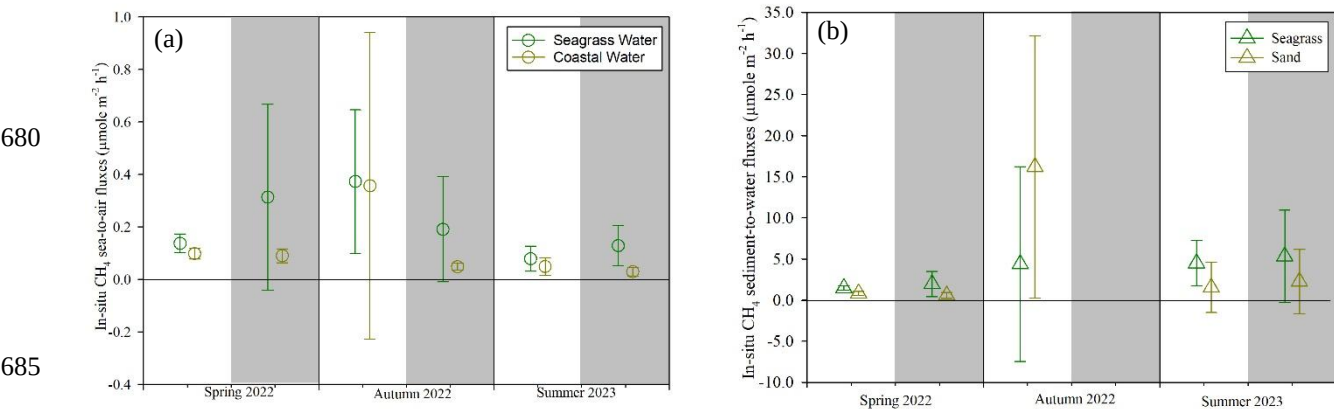


Figure 6. Diurnal variation of CH₄ (a) sea-to-air fluxes ($\mu\text{mole m}^{-2} \text{h}^{-1}$; n=226) and (b) sediment-to-water fluxes ($\mu\text{mole m}^{-2} \text{h}^{-1}$; n=284) in seagrass water and coastal water. Bright areas indicate daytime, and grey areas indicate nighttime.

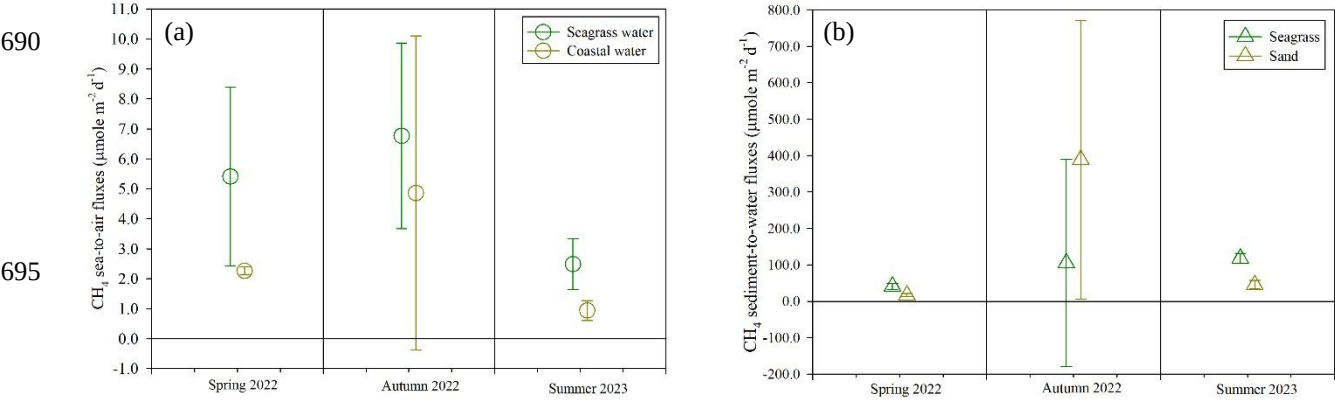


Figure 7. Seasonal variation of CH₄ (a) sea-to-air fluxes (μmole m⁻² d⁻¹; n=226) and (b) sediment-to-water fluxes (μmole m⁻² d⁻¹; n=284) in seagrass water and coastal water.

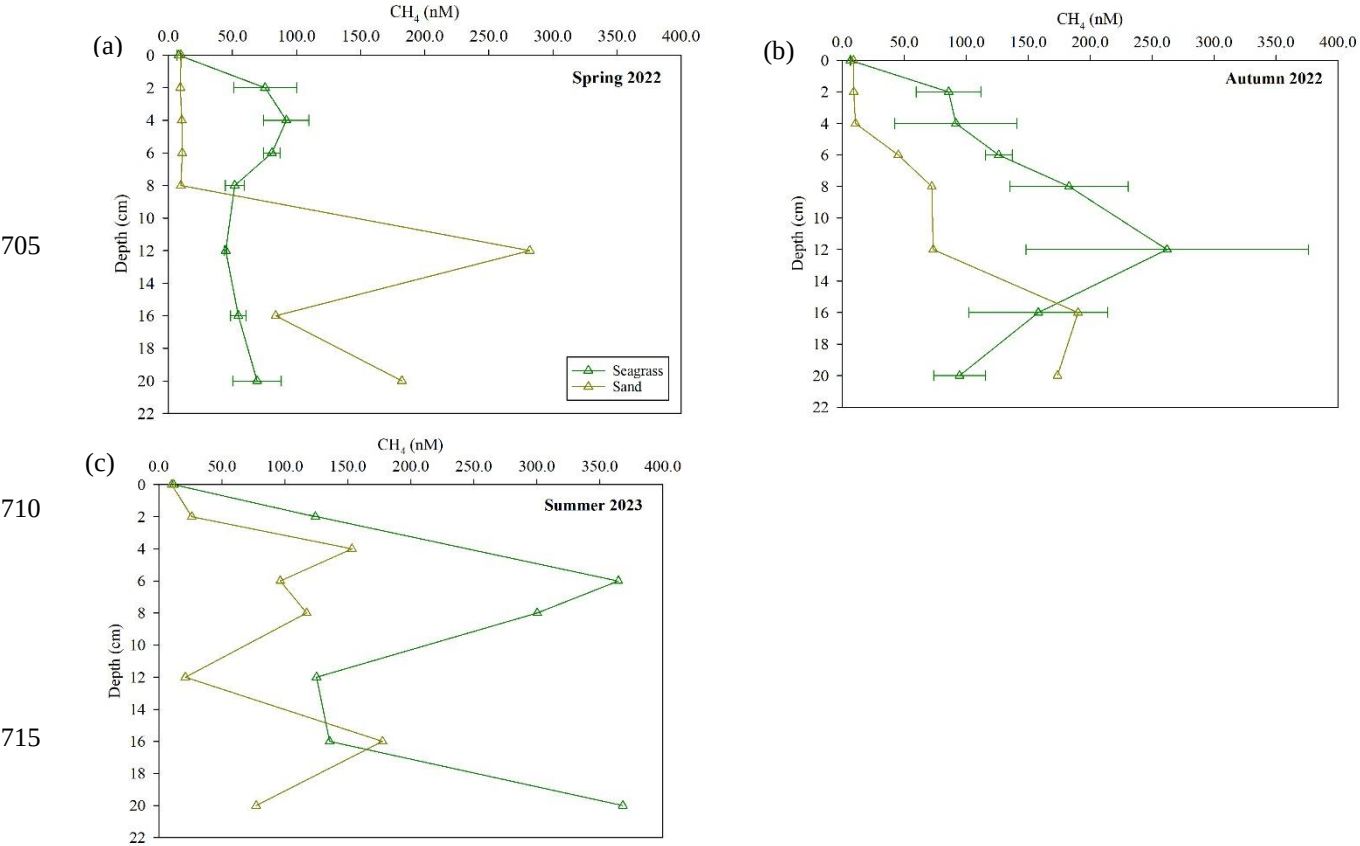


Figure 8. CH₄ concentration profiles in porewater: (a) spring 2022 (n=32), (b) autumn 2022 (n=32), and (c) summer 2023 (n=15). Error bars represent the range of duplicate samples; error bars are absent for depth intervals where only single sample was available.