



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 15 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 20 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 25 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.

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 30 (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 1850–1900 levels during the period 2011–2020 (IPCC, 2021). Achieving climate



neutrality requires both reducing GHG emissions and enhancing natural GHG sinks. Additionally, long-term carbon storage is necessary to offset unavoidable residual emissions. One effective strategy for countries is to preserve and expand natural
35 carbon sinks (Howard et al., 2023). Coastal ecosystems, such as mangroves, seagrasses, and salt marshes, store substantial amounts of carbon in their sediments and play a vital role in climate change mitigation. These ecosystems are collectively known as "Blue Carbon ecosystems".

Seagrass meadows 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). Through
40 photosynthesis, they convert light energy into organic matter while utilizing dissolved inorganic carbon, enabling long-term carbon sequestration in their sediments for centuries (Rosentreter et al., 2021b; Yau et al., 2023). 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, these ecosystems are also recognized as sources of CH₄, a potent GHG with a sustained-flux global warming potential (SGWP) 27–80 times greater than
45 that of CO₂ on a mass basis (IPCC, 2021). Depending on seagrass species, regions and geography, CH₄ emissions from seagrass meadows could offset 0.5–33.4% of the blue carbon sequestered in sediments (Rosentreter et al., 2021b; Yau et al., 2023; Eyre et al., 2023). More broadly, the coastal ocean is a global hotspot for CH₄ emissions, accounting for 75% of oceanic CH₄ emissions (Weber et al., 2019), with continental shelves alone contributing approximately 13 Tg CH₄ yr⁻¹ (Bange et al., 1994). In coastal waters, CH₄ is primarily produced in sediments through the anaerobic microbial degradation of organic carbon via
50 methanogenesis (Arndt et al., 2013). 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 CH₄ production in seagrass meadows is considered a minor pathway (Schorn et al., 2022), the CH₄ generated in sediments can be released into the
55 overlying water column via diffusion or advective exchange, potentially contributing to CH₄ emissions from these ecosystems (Saunois et al., 2020). Seagrass meadows are vital to coastal carbon cycling, but their function as CH₄ sources adds complexity to evaluating their overall climate impact. While some studies suggest that seagrass meadows generally emit less CH₄ compared to mangroves and salt marshes (Yau et al., 2023), site-specific conditions can lead to substantial variability in emissions (Oreska et al., 2020). CH₄ production in seagrass meadows is driven by various biogeochemical processes, including
60 organic matter decomposition, microbial interactions, and sedimentary conditions, which influence the balance between carbon sequestration and GHG emissions (Saunois et al., 2020; Schorn et al., 2022; Sogin et al., 2022; Arndt et al., 2013). Given that CH₄ is a potent GHG capable of offsetting some of the climate benefits of seagrass carbon storage, accurately quantifying seagrass-associated CH₄ fluxes is essential for assessing their net climate impact. Integrating these emissions into both local and global CH₄ budget assessments is crucial for a comprehensive understanding of seagrass meadows' role in climate
65 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).

70 This study provides the first comprehensive assessment of diel, seasonal, and annual CH₄ dynamics in Taiwan's seagrass ecosystems, with a focus on the Haikou seagrass meadow. Through a series of intensive field campaigns, we combined surface water sampling, in situ benthic chamber incubations, and porewater profiling to investigate CH₄ processes in both seagrass and adjacent bare sand habitats. This integrated approach allowed us to capture patterns of CH₄ 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.

75 2. Materials and Methods

2.1 Study area and sampling periods

The study site is located at Haikou, Checheng Township, Pingtung County, Taiwan (22°5'21.830"N, 120°42'42.408"E; Figure 1). 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). 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 from June 13 to 17 (summer) in 2023. Due to 80 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.

2.2 In situ chamber incubation system

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 90 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 sampling needs, wave conditions, and weather. 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 6:00, 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

Seawater samples for CH₄ analysis were collected 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 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 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, transported to the lab, and stored in darkness at 4 °C. 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 The CH₄ saturation ratio and water-air fluxes

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

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

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., 2024).

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

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

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

130 2.5 The benthic CH_4 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:

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

$$135 \quad F_{\text{sediment-water}} = \left(\frac{\Delta C}{\Delta t} \right) \times \left(\frac{V_{\text{chamber}}}{A_{\text{chamber}}} \right) \quad (5)$$

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 CH_4 concentration (nmol L^{-1}), during the incubation period Δt (hours); V_{chamber} is the volume of overlying water in the chamber (m^3); A_{chamber} is the area of the chamber (m^2).

3. Results and Discussion

140 3.1 Seasonal 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–
145 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 CH_4 concentrations in seagrass waters exhibited clear seasonal and diurnal variability, with higher averages at night
150 and lower values during the day, except in autumn 2022 when a severe weather event disrupted this pattern. The daytime suppression of CH_4 was likely associated with elevated dissolved oxygen saturation driven by photosynthesis. Coastal waters exhibited lower and more stable CH_4 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
155 the much shallower seagrass habitats that range from about 0.5 to 1.5 m in depth. Alternatively, CH_4 released from sediments may have been oxidized before reaching the coastal water surface.



3.2 Seasonal 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–
160 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).
165 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
170 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.

175 3.3 Seasonal sediment CH₄ 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
185 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
190 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
195 create anoxic sediment environments where methanogenic archaea thrive, promoting higher CH₄ production compared to the
more oxygenated conditions of sandy sediments (Saderne 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.
200 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
205 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
210 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).

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
215 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
220 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.

225 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).
230 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
235 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).

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
240 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
245 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 mol CH₄ yr⁻¹ into the overlying seawater, whereas the water column emitted only about 78.3 mol CH₄ yr⁻¹ to the
250 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.



255 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
260 transport (Li et al., 2021). Consequently, seagrass sediments generally support higher CH₄ concentrations and more regulated
fluxes than unvegetated sands (George et al., 2020; Schorn 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
265 (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.,
2018), where tropical seagrass meadows exhibited elevated CH₄ emissions, further amplified by warming conditions and linked
to methylotrophic 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
270 the global scale, seagrass ecosystems are generally net sources of CH₄ with mean flux of 79.0 μmol m⁻² 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 methylotrophic 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., 2008).
275 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,
280 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
285 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
290 essential to include CH₄ in comprehensive blue carbon assessments.

4. Conclusions

This study presents the first integrated assessment of seasonal and annual CH₄ dynamics 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
295 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
300 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
305 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
310 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.

Data availability

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

Author contributions

315 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,



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320 **Competing interests**

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

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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		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	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		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	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		0.9 ± 0.3	
Annual	Seagrass Water							4.9 ± 2.2	
	Coastal Water							2.7 ± 2.0	

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

Location	Species	Site	Climate	Method	Sea-to-air Flux (μmol m ⁻² d ⁻¹)	Method	Sediment-to-water Flux (μmol m ⁻¹ d ⁻¹)	References
Wallagoot, Australia	<i>Ruppia megacarpa</i>	Mouth of estuary	Temperate	Continuous surface water	33.8			
	<i>Halophila ovalis</i>						45.4	(Camillini, 2020)
Wallis Lake, Australia	<i>Posidonia australis</i>	Mouth of estuary	Temperate			Benthic chamber	279.3	
	<i>Zostera muelleri</i>						46.0	
Swan Bay, Australia	<i>Zostera muelleri</i>	Tidal lagoon	Temperate	Continuous surface water	10.5			(Ollivier et al., 2022)
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	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		113.8		73.3	
Cadaques, Spain	<i>Posidonia oceanica</i>	Coastal bay	Temperate	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	Dynamic flux chamber	307.2			(Bahlmann et al., 2015)
Baltic Sea, Finland	<i>Zostera marina</i>	Coastal bay	Temperate				1.6 ± 1.6	
Kattegat, Denmark	<i>Zostera marina</i>	Fjord-coastal Bay	Temperate			Benthic chamber	3.4 ± 0.5	(Asplund et al., 2022)
Skagerrak, Sweden	<i>Zostera marina</i>	Coastal bay	Temperate				2.5 ± 2.8	
Mediterranean Sea, Italy	<i>Posidonia oceanica</i>	Coastal bay	Temperate			Porewater	106.0	(Schorn et al., 2022)
Swan lake, Shandong, China	<i>Zostera marina</i> , <i>Zostera japonica</i>	Coastal lagoon	Temperate	Water samples	5.5 ± 8.4			(Tan et al., 2025)
	<i>Enhalus acoroides</i>						96.2	
	<i>Thalassodesmion 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, 2017)
	<i>Halophila</i> , <i>Halodule</i> spp.						61.0	
	<i>Halodule uninervis</i>						48.1	
	<i>Cymodocea serrulate</i> ,						401.3	



Chilika Lagoon, India	<i>Halodule uninervis</i> <i>Halodule sp.</i> , <i>Halophila sp</i>	Tidal lagoon	Tropical	Discrete water samples	120.0			(Banerjee et al., 2018)
Awerange Bay, Indonesia	<i>Enhalus acoroides</i> <i>Enhalus acoroides</i>	Coastal bay	Tropical			Sediment core	95.7 ± 95.4	(Alongi et al., 2008)
Koh Mook, Thailand	<i>Thalassia hemprichii</i> <i>Thalassia hemprichii</i>	Coastal inlet	Tropical	Benthic chamber	3.1 2.0			(Halim et al., 2024)
Haikou, Taiwan	<i>Halodule hemprichii</i> , <i>Halodule pinifolia</i>	Coastal inlet	Tropical	Discrete water samples	4.9 ± 2.2	Benthic chamber	88.2 ± 41.2	This study

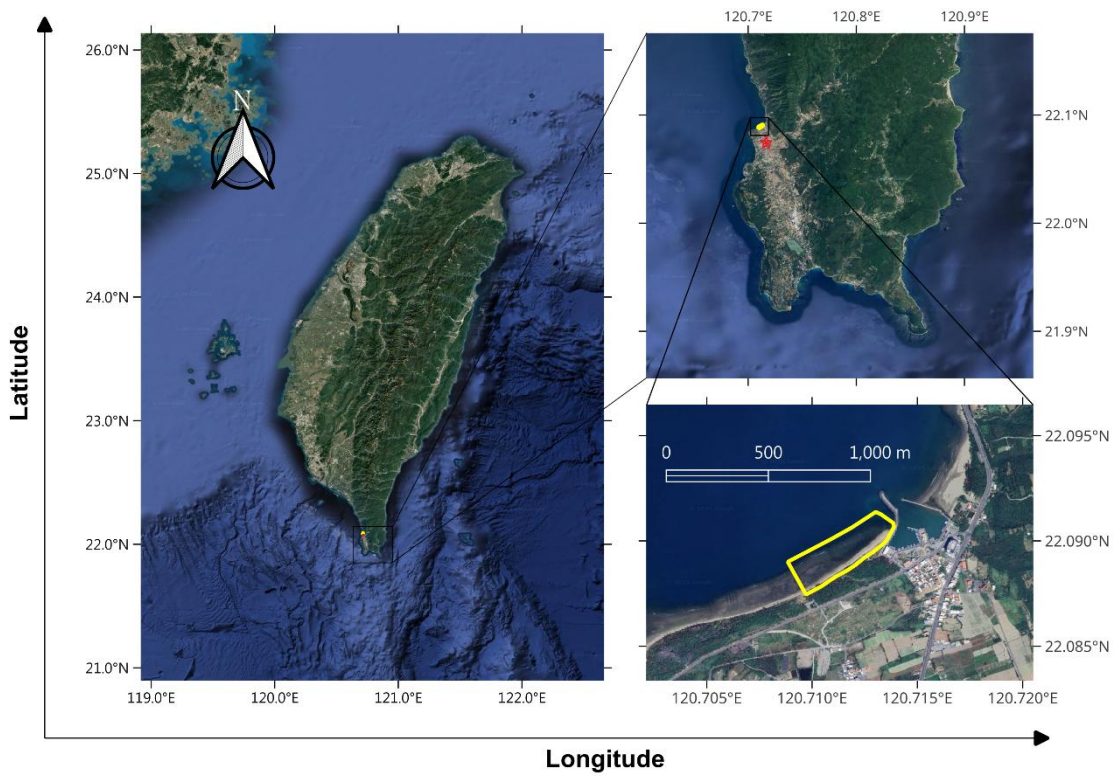
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535 Figure 1. Study area. (The yellow rectangle indicates the seagrass meadow area, while the red star marks the Checheng Weather Station.)

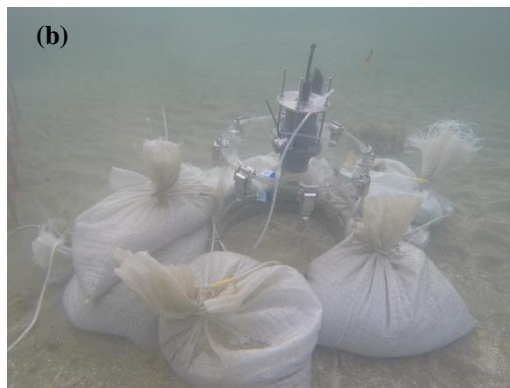
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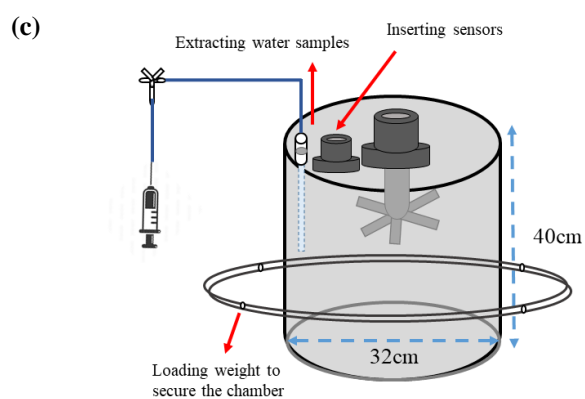
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Figure 2. Benthic chamber in situ incubation systems deployed in (a) seagrass and (b) bare sediment environments, with (c) schematic diagram illustrating the chamber design.

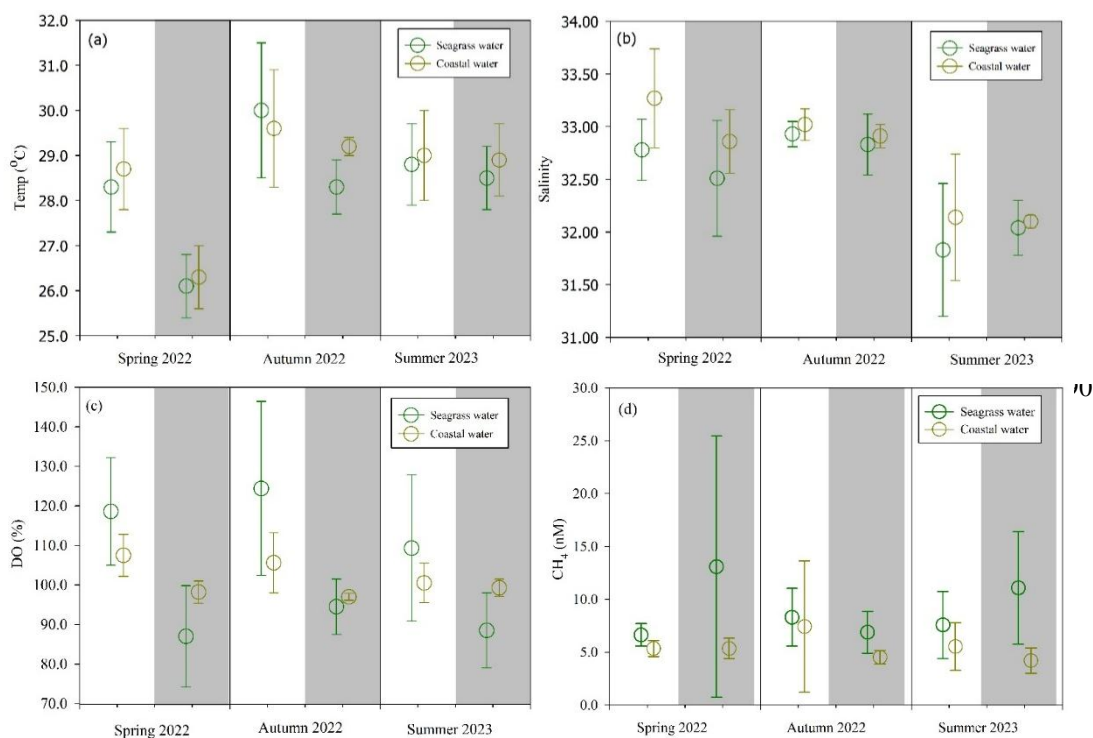
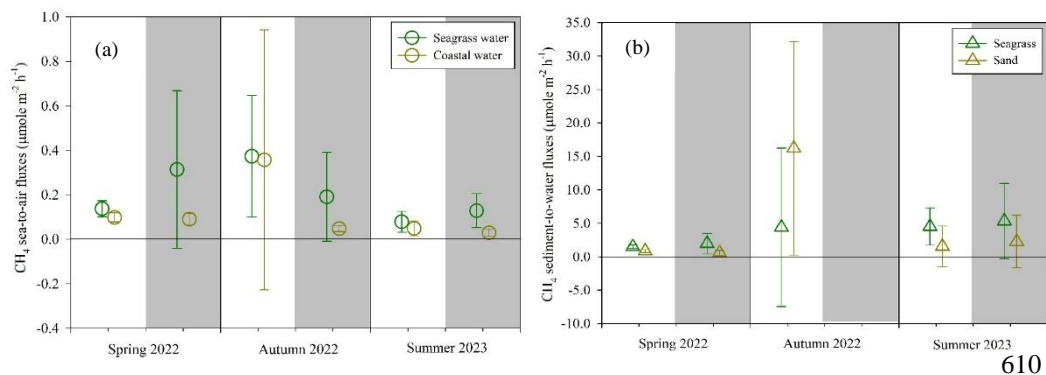


Figure 3. Seasonal environmental conditions of (a) temperature, (b) salinity, (c) DO%, and (d) CH₄ concentrations in seagrass water and coastal water. Bright areas indicate daytime, and grey areas indicate nighttime.

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Figure 4. 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.

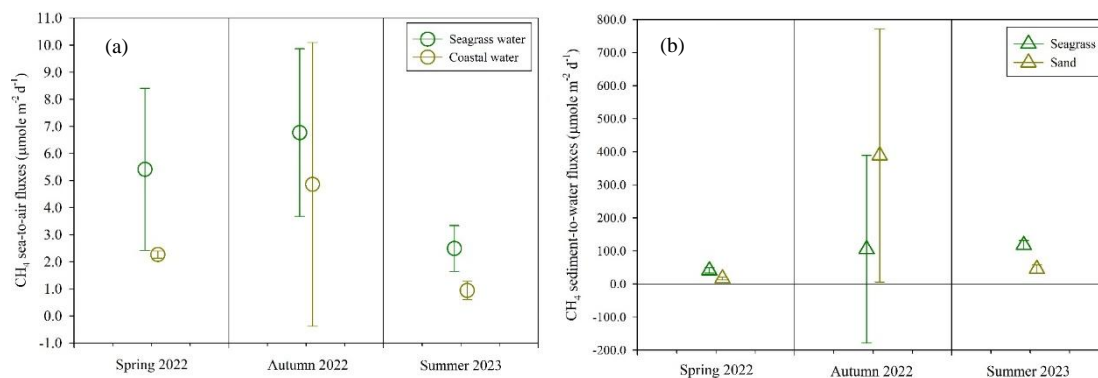


Figure 5. Seasonal variation of CH₄ (a) sea-to-air fluxes ($\mu\text{mole m}^{-2} \text{d}^{-1}$; n=226) and (b) sediment-to-water fluxes ($\mu\text{mole m}^{-2} \text{d}^{-1}$; n=284) in seagrass water and coastal water.

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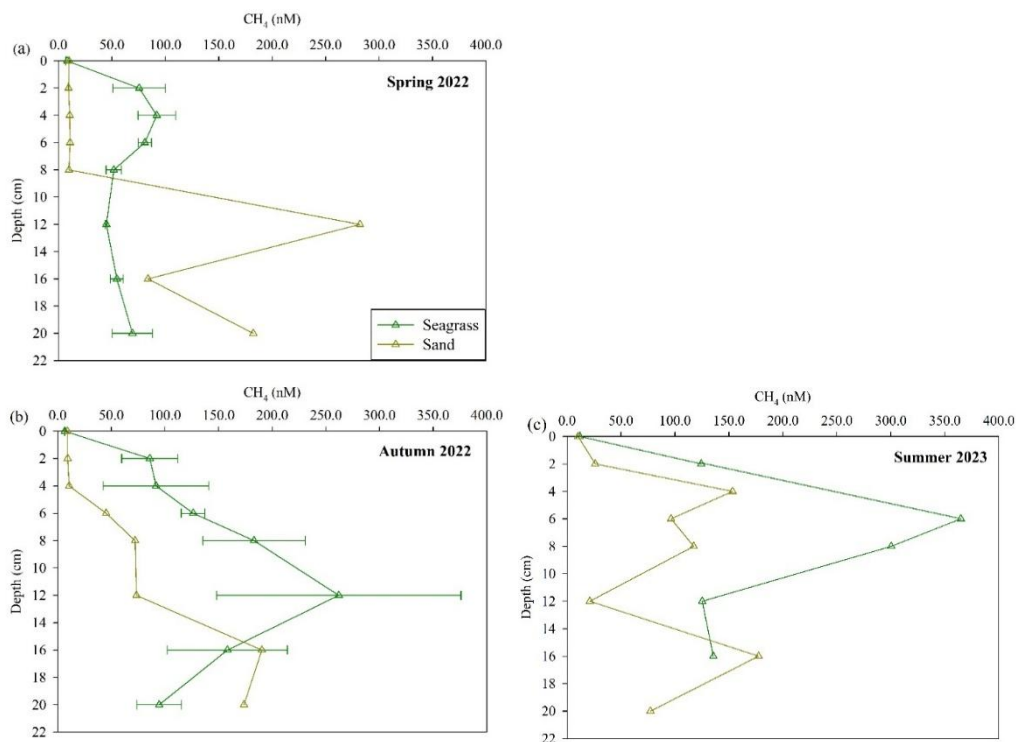


Figure 6. CH₄ concentration profiles in porewater: (a) spring 2022 (n=32), (b) autumn 2022 (n=32), and (c) summer 2023 (n=15).

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