

# Methane emissions in seagrass meadows as a small offset to carbon sequestration

Yvonne Yu Yan Yau<sup>1</sup>, Gloria Reithmaier<sup>2</sup>, Claudia Majtenyi-Hill<sup>1</sup>, Nerea Piñeiro-Juncal<sup>3</sup>, Martin Dahl<sup>2</sup>, Miguel Angel Mateo<sup>4</sup>, Stefano Bonaglia<sup>1</sup>, Oscar Serrano<sup>5</sup>, and Isaac Santos<sup>1</sup>

<sup>1</sup>University of Gothenburg

<sup>2</sup>Unknown

<sup>3</sup>University of Aveiro

<sup>4</sup>Consejo Superior Investigaciones Cientificas

<sup>5</sup>Edith Cowan University

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## Abstract

Seagrass meadows are effective carbon sinks due to their high primary production and sequestration in sediments. However, methane (CH<sub>4</sub>) fluxes can partially counteract their carbon sink capacity. Here, we measured diffusive sediment-water and air-sea CO<sub>2</sub> and CH<sub>4</sub> fluxes in a coastal embayment dominated by *Posidonia oceanica* in the Mediterranean Sea. High resolution timeseries observations revealed large spatial and temporal variability in CH<sub>4</sub> concentrations (2 to 36 nM). Higher emissions were observed in an area with dense seagrass meadows. A 6 - 40% decrease of CH<sub>4</sub> concentration in the surface water around noon indicates that photosynthesis likely limits CH<sub>4</sub> fluxes. Sediments were the major CH<sub>4</sub> source as implied from radon (a natural porewater tracer) observations and evidence for methanogenesis in deeper sediments. CH<sub>4</sub> sediment-water fluxes ( $0.1 \pm 0.1 - 0.4 \pm 0.1 \mu\text{mol m}^{-2} \text{d}^{-1}$ ) were higher than average water-air CH<sub>4</sub> emissions ( $0.12 \pm 0.10 \mu\text{mol m}^{-2} \text{d}^{-1}$ ), suggesting that dilution and CH<sub>4</sub> oxidation in the water column could reduce net CH<sub>4</sub> fluxes into the atmosphere. Overall, relatively low air-sea CH<sub>4</sub> fluxes at this likely represent net emissions from subtidal seagrass habitats sites, which are not influenced by nearby allochthonous CH<sub>4</sub> sources. The local CH<sub>4</sub> emissions in *P. oceanica* offset less than 1% of the carbon burial in sediments ( $142 \pm 69 \text{ g CO}_2\text{eq m}^{-2} \text{yr}^{-1}$ ). Combining our results with earlier observations in other seagrass meadows worldwide reveals that global CH<sub>4</sub> emissions within seagrass meadows only offset a small fraction (<2%) of carbon sequestration in sediments.

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1           **Methane emissions in seagrass meadows as a small offset to carbon sequestration**

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3 Piñeiro-Juncal<sup>2,4</sup>, Martin Dahl<sup>2,6</sup>, Miguel Angel Mateo<sup>2,3</sup>, Stefano Bonaglia<sup>1</sup>, and Isaac R.  
4 Santos<sup>1,7</sup>

5

6 <sup>1</sup> Department of Marine Sciences, University of Gothenburg, Gothenburg, Sweden

7 <sup>2</sup> Centro de Estudios Avanzados de Blanes, Consejo Superior de Investigaciones Científicas,  
8 Blanes, Spain

9 <sup>3</sup> School of Science and Centre for Marine Ecosystems Research, Edith Cowan University,  
10 Joondalup, WA, Australia

11 <sup>4</sup> Department of Biology & CESAM – Centre for Environmental and Marine Studies,  
12 University of Aveiro, Aveiro, Portugal

13 <sup>5</sup> CRETUS, EcoPast (GI-1553), Facultade de Biología, Universidade de Santiago de  
14 Compostela, Campus Sur s/n, Santiago de Compostela, 15782, Spain

15 <sup>6</sup> Södertörn University, School of Natural Sciences, Technology and Environmental Studies,  
16 Environmental Science. Stockholm University, Sweden

17 <sup>7</sup> National Marine Science Centre, Southern Cross University, Australia

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19 Corresponding author: Yvonne Yu Yan Yau ([yvonne.yau@gu.se](mailto:yvonne.yau@gu.se))

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21           **Key Points:**

- 22           • High resolution CH<sub>4</sub> observations reveal diel cycles linked to seagrass productivity
- 23           • Sediments were the main CH<sub>4</sub> source in both living and dead seagrass areas
- 24           • CH<sub>4</sub> emissions were a small offset to seagrass C sequestration on local and global
- 25           scales

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36 **Abstract**

37 Seagrass meadows are effective carbon sinks due to their high primary production and  
38 sequestration in sediments. However, methane (CH<sub>4</sub>) fluxes can partially counteract their  
39 carbon sink capacity. Here, we measured diffusive sediment-water and air-sea CO<sub>2</sub> and CH<sub>4</sub>  
40 fluxes in a coastal embayment dominated by *Posidonia oceanica* in the Mediterranean Sea.  
41 High resolution timeseries observations revealed large spatial and temporal variability in CH<sub>4</sub>  
42 concentrations (2 to 36 nM). Higher emissions were observed in an area with dense seagrass  
43 meadows. A 6 – 40% decrease of CH<sub>4</sub> concentration in the surface water around noon  
44 indicates that photosynthesis likely limits CH<sub>4</sub> fluxes. Sediments were the major CH<sub>4</sub> source  
45 as implied from radon (a natural porewater tracer) observations and evidence for  
46 methanogenesis in deeper sediments. CH<sub>4</sub> sediment-water fluxes ( $0.1 \pm 0.1 - 0.4 \pm 0.1 \mu\text{mol}$   
47  $\text{m}^{-2} \text{d}^{-1}$ ) were higher than average water-air CH<sub>4</sub> emissions ( $0.12 \pm 0.10 \mu\text{mol m}^{-2} \text{d}^{-1}$ ),  
48 suggesting that dilution and CH<sub>4</sub> oxidation in the water column could reduce net CH<sub>4</sub> fluxes  
49 into the atmosphere. Overall, relatively low air-sea CH<sub>4</sub> fluxes at this likely represent net  
50 emissions from subtidal seagrass habitats sites, which are not influenced by nearby  
51 allochthonous CH<sub>4</sub> sources. The local CH<sub>4</sub> emissions in *P. oceanica* offset less than 1% of  
52 the carbon burial in sediments ( $142 \pm 69 \text{ g CO}_{2\text{eq}} \text{m}^{-2} \text{yr}^{-1}$ ). Combining our results with earlier  
53 observations in other seagrass meadows worldwide reveals that global CH<sub>4</sub> emissions within  
54 seagrass meadows only offset a small fraction (<2%) of carbon sequestration in sediments.

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56 **Plain language Summary**

57 Seagrass meadows are important hotspots for carbon storage in the sediment. Part of the  
58 sediment carbon can be emitted as the greenhouse gases carbon dioxide and methane (CH<sub>4</sub>).  
59 Methane has a 45 – 96 times more powerful global warming effect than carbon dioxide. If  
60 seagrass meadows release CH<sub>4</sub>, the emissions counteract their climate mitigation potential.  
61 We measured greenhouse gas concentrations and fluxes in a seagrass-dominated  
62 Mediterranean embayment. Low CH<sub>4</sub> coincided with the increase of oxygen produced  
63 through seagrass photosynthesis. Areas with dense seagrass meadows had lower CH<sub>4</sub>  
64 emissions. Overall, the seagrass-dominated bay was a small source of CH<sub>4</sub> that can offset  
65 only <1% of carbon buried in sediments. Hence, seagrass meadows remain an effective  
66 carbon sink.

## 67 **1 Introduction**

68 Seagrass meadows are effective carbon sinks recognized for their potential role in climate  
69 change mitigation (Fourqurean et al., 2012; Lovelock & Duarte, 2019; Mcleod et al., 2011).  
70 Seagrass meadows sequester carbon dioxide (CO<sub>2</sub>) through photosynthesis (Van Dam et al.,  
71 2021) and trap allochthonous particles within their canopy (Gacia et al., 2002). Part of this  
72 carbon is then stored as biomass and as organic carbon in sediments for centuries and even  
73 millennia (Serrano et al., 2016, 2021). Seagrass meadows account for 10 – 18% of the total  
74 carbon burial (27 44 Tg C y<sup>-1</sup>) in the ocean even though they cover only 0.1% of the global  
75 ocean area (Kennedy et al., 2010). In addition, about 5% of the particulate organic carbon and  
76 dissolved organic carbon produced within seagrass habitats is exported beyond the meadows  
77 and stored in the deep ocean (Duarte & Krause-Jensen, 2017). Seagrass meadows are  
78 considered an important blue carbon ecosystem that should be protected and restored to  
79 mitigate anthropogenic CO<sub>2</sub> emissions

80

81 *Posidonia oceanica* is the dominant seagrass species along the Mediterranean coast and an  
82 important blue carbon ecosystem (Telesca et al., 2015). *P. oceanica* is a slow-growing and  
83 long-living seagrass, which accumulates  $84 \pm 20 \text{ g C m}^{-2} \text{ yr}^{-1}$  of organic carbon in the  
84 sediment (Serrano et al., 2016). A special feature of *P. oceanica* is the formation of thick (up  
85 to 6.5 m) and old (up to millennia) organic detritus known as *mattes*, storing large quantities  
86 of organic matter in the sediments (Lo Iacono et al., 2008; Mateo et al., 1997). These dead  
87 mattes can remain as important carbon and biogeochemical sinks even 30 years after seagrass  
88 death of the meadow (Apostolaki et al., 2022). Due to their slow decay rates and recalcitrant  
89 nature, *P. oceanica* is one of the largest blue carbon sinks among seagrass species (Gacia et  
90 al., 2002; Kaal et al., 2018; Serrano et al., 2018). However, natural and human disturbances  
91 such as moorings and coastal development destroy seagrass meadows potentially leading to  
92 reduction of carbon stocks and increased emissions of CO<sub>2</sub> and CH<sub>4</sub> to the atmosphere  
93 (Carnell et al., 2020; Lyimo et al., 2018).

94

95 The coastal ocean is a hotspot of CH<sub>4</sub> emissions, contributing with 75% of the global oceanic  
96 CH<sub>4</sub> emissions (Weber et al., 2019). While seagrass meadows store organic carbon, the high  
97 sediment organic matter content also favors methane (CH<sub>4</sub>) production (Rosentreter, Al-Haj,  
98 et al., 2021). CH<sub>4</sub> is produced during anaerobic microbial degradation of organic carbon via  
99 methanogenesis (Martens & Klump, 1980) usually after all the other energetically favorable  
100 electron acceptors become depleted in sediments (Froelich et al., 1979). Thus, oxygen,  
101 nitrate, metal oxide and sulphate availability in marine sediments can limit methanogenesis  
102 and CH<sub>4</sub> emissions (Egger, Kraal, et al., 2016). The presence of methylated compounds in  
103 seagrass rhizosphere provide another pathway for CH<sub>4</sub> production, even in dead seagrass  
104 meadows (Schorn et al., 2022). The net CH<sub>4</sub> emission is also controlled by production and  
105 oxidation in sediment and water column before reaching the atmosphere (Egger, Lenstra, et  
106 al., 2016; Ward et al., 1987). Understanding both sediment-water and air-sea fluxes can  
107 provide insight on net CH<sub>4</sub> fluxes to the atmosphere.

108 Since CH<sub>4</sub> is a potent greenhouse gas with 45–96 times greater sustained-flux warming  
109 potential (SGWP) than CO<sub>2</sub> (Neubauer & Megonigal, 2015), the efficiency of seagrasses as a  
110 carbon sink can be partially offset by CH<sub>4</sub> emissions. Although measurements of CH<sub>4</sub> fluxes

111 have been widely performed in mangroves (Call et al., 2019), saltmarshes (Yau et al., 2022),  
112 and other coastal ecosystems (Borges & Abril, 2011), CH<sub>4</sub> fluxes in seagrass meadows  
113 remain poorly constrained across multiple spatial and temporal scales. The air-sea and  
114 sediment-water CH<sub>4</sub> fluxes from seagrass ranged from 0 to 400 μmol m<sup>-2</sup> d<sup>-1</sup>, resulting in  
115 global upscaled fluxes of 0.18 Tg CH<sub>4</sub> per year (Al-Haj et al., 2022). Several seagrass  
116 meadow CH<sub>4</sub> flux estimates considered sediment-water fluxes, obtained from benthic  
117 chambers and sediment incubation approaches, to be equivalent to air-sea fluxes. This  
118 assumes that sediment CH<sub>4</sub> propagates through the shallow water column and reaches the  
119 atmosphere unmodified.

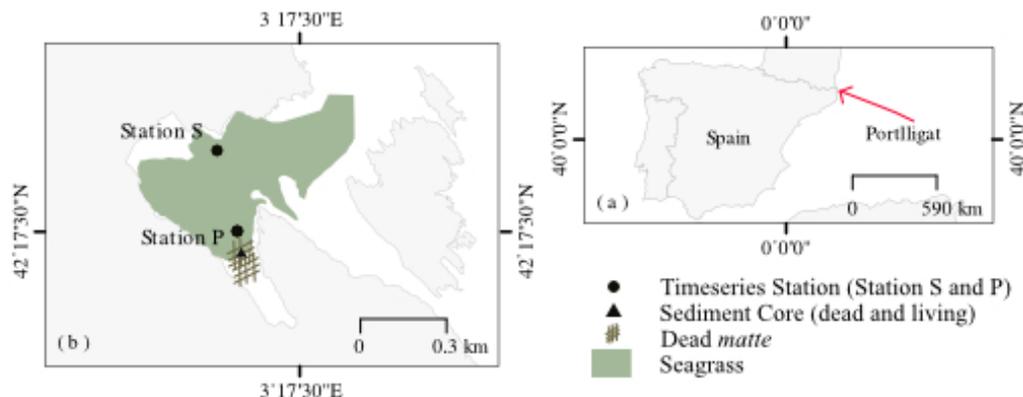
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121 Here, we report high resolution timeseries observations of dissolved CH<sub>4</sub> over multiple diel  
122 cycles and estimate sediment-water and air-sea CH<sub>4</sub> fluxes in *P. oceanica* meadows at a  
123 Mediterranean bay. We quantified air-sea CO<sub>2</sub> and CH<sub>4</sub> fluxes above the seagrass using  
124 automated, *in situ* surface water observations (including <sup>222</sup>Rn measurements, a natural  
125 porewater tracer), and at the sediment-water interface using sediment cores. This study aims  
126 to (1) estimate sediment-water CH<sub>4</sub> fluxes, (2) evaluate the spatial and diel variability of air-  
127 sea CH<sub>4</sub> fluxes, (3) assess the fate of CH<sub>4</sub> by comparing CH<sub>4</sub> sediment-water fluxes and air-  
128 sea fluxes, and (4) examine whether CH<sub>4</sub> emissions can partially offset carbon sequestration  
129 in seagrass on both local and global scales.

## 130 **2 Materials and Methods**

### 131 **2.1 Sampling location**

132 Field observations were performed at Portlligat Bay (42°17'32" N, 3°7'28" E) on the  
133 northeast coast of Spain in the Mediterranean Sea. The bay is shallow ranging from 2 to 10  
134 m, with < 0.5 m tidal ranges (Serrano et al., 2012). *P. oceanica* is the dominant seagrass  
135 species in the bay, covering 41% of the area (0.12 km<sup>2</sup>). The seabed is irregular with mounds  
136 of matte deposits (ranging from 3.5 to 6 m in thickness) formed by *P. oceanica* debris  
137 intertwined with fine to medium sands (Lo Iacono et al., 2008). Dense *P. oceanica* (> 600  
138 shoots m<sup>-2</sup>) were found within the center and north of the bay, whereas patchy seagrass  
139 meadows within sand and dead mattes were found at the south of the bay. Anthropogenic  
140 disturbances in the embayment are limited to boating and the deployment of environmentally  
141 friendly moorings in the center of the bay. The nature of the matte with the presence of dense  
142 roots, rhizomes and sheaths remains of *P. oceanica* limits burrowing activities in the  
143 sediments. An ephemeral stream is located at the northeast edge of the bay, but there are no  
144 permanent rivers supplying freshwater to the bay.



146

147 **Figure 1.** Study site map. (a) Location of Portlligat bay; (b) Portlligat bay with location of  
 148 timeseries Stations S and P, sediment core of living and dead seagrasses, extent of *Posidonia*  
 149 *oceanica* meadows (shaded green) modified from (Leiva-Dueñas et al., 2018) and the dead  
 150 *matte*.

151

## 152 2.2 Timeseries and spatial survey

153 Two timeseries stations were deployed simultaneously during 11<sup>th</sup> to 18<sup>th</sup> September 2021  
 154 (Figure 1). Station S was in a healthy seagrass-dominated area (42°17'38" N, 3°17'19" E),  
 155 whilst Station P was surrounded by patchy seagrass meadows, including dead seagrass areas  
 156 (42°17'29" N, 3°17'22" E). Precipitation events were recorded from 01:00 to 09:00 on 16<sup>th</sup>  
 157 September with a maximum 2.9 cm hr<sup>-1</sup>.

158 Water depth, salinity and temperature were measured every 5 minutes (Levellogger 5 LTC,  
 159 Solinst), whereas dissolved oxygen (DO) was recorded at 1 min intervals (miniDOT, PME),  
 160 which were installed close to the sediment surface. Radon was measured with a <sup>222</sup>Rn-air  
 161 analyzer (RAD7), while CO<sub>2</sub> and CH<sub>4</sub> were measured with a greenhouse gas analyzer (LI-  
 162 7810, LI-COR). Both were connected to a DurrIDGE shower head gas exchange device as  
 163 described elsewhere (Webb et al. 2016 and references there in). A water pump was attached  
 164 at the side of the boat (~50 cm deep) to sample surface water at 3 L min<sup>-1</sup> to the showerhead  
 165 gas exchange. There were data gaps in the patchy seagrass due to instrument failure (days  
 166 13<sup>th</sup> and 14<sup>th</sup> September 2021). CO<sub>2</sub> and CH<sub>4</sub> concentrations were recorded at 1-second  
 167 intervals and radon at 30 min intervals. Time lags of 30, 10 and 30 minutes were applied to  
 168 <sup>222</sup>Rn, CO<sub>2</sub> and CH<sub>4</sub> respectively to account for gas equilibrium between water and the closed  
 169 air loop (Webb et al., 2016). The data were aggregated into 5 minutes intervals.

170 A spatial survey was conducted to measure <sup>222</sup>Rn, CO<sub>2</sub> and CH<sub>4</sub> across the bay covering a  
 171 track of 1.5 km on 18<sup>th</sup> September 2021 from 16:00 to 17:30 using the same experimental  
 172 setup as described above. CH<sub>4</sub> fluxes for the whole bay area were found using inverse  
 173 distance weighted interpolation methods, from which an average was obtained.. Solubility of  
 174 CO<sub>2</sub> and CH<sub>4</sub> was calculated as a function of temperature and salinity using Weiss (1974) and  
 175 Yamamoto et al. (1976), respectively, and normalized to the Schmidt number as described in  
 176 Wanninkhof (2014). Meteorological parameters such as radiation, wind speed and

177 precipitation were obtained from nearest automated station of Roses (42° 16' 20.56" N, 3° 11'  
178 1.16" E) from the government of Catalonia.

179

### 180 **2.3 Sediment and porewater analysis**

181 Six sediment cores were collected by manual hammering of PVC pipes (1 m long and 60 mm  
182 inner diameter) in both dead and living seagrass (Figure 1). To sample for dissolved CH<sub>4</sub> in  
183 porewater, a push-core with pre-drilled holes (1 cm diameter) was used to minimize the  
184 oxidation during sampling. 3mL of wet sediment were extracted using a cut-off plastic  
185 syringe and transferred into 22mL gas-tight vials containing 10 mL of a 1M NaOH solution  
186 to preserve methane. The vials were then crimped immediately using aluminum caps with  
187 butyl rubber stoppers. Back in the lab, all headspace from each vial (7–10 mL) were  
188 transferred into a second N<sub>2</sub> flushed vial using a gas-tight syringe. The headspace CH<sub>4</sub>  
189 concentrations were then measured using a gas chromatographer (Thermo Scientific Trace  
190 1300) equipped with flame ionization detector. Reference gas standards of 1.9 ppm and 50  
191 ppm (Air Liquide Gas AB) were used for instrument calibration. The porewater methane  
192 concentrations were calculated from the measured headspace concentrations (Hoehler et al.,  
193 2000), (Equation 1):

$$194 \quad [CH_4] = \frac{P \cdot V_H}{R \cdot T \cdot \phi \cdot V_S} \quad (1)$$

195 where  $[CH_4]$  is the porewater CH<sub>4</sub> concentration (nM),  $P$  is the methane partial pressure  
196 inside the vial (atm),  $V_H$  and  $V_S$  are the volume of headspace in each vial and the sediment  
197 sample (mL),  $R$  is the universal gas constant (L atm K<sup>-1</sup> mol<sup>-1</sup>),  $T$  is the laboratory  
198 temperature (°C) and  $\phi$  is the sediments porosity in each sediment layer. Sediment porosity  
199 was calculated from water content (weight difference of wet and dry sample weight after  
200 drying at 100°C) and sediment bulk density (Lengier et al., 2021)

201 Porewater for DIC was extracted from sediment cores using Rhizon samplers (Rhizosphere  
202 research product). Approximately 10–15 mL of porewater was collected. DIC samples were  
203 collected in 12 mL exetainers without headspace. DIC concentrations were analyzed by Total  
204 Dissolved Inorganic Carbon Analyzer (Appollo AS-C5) at the University of Gothenburg.  
205 Certified reference material (CRM from Dickson Laboratory, Scripps Institute of  
206 Oceanography) was used as the standard. The analytical precision was better than 2% for  
207 porewater.

208 The organic matter content of the sediment layers was estimated based on the Loss of  
209 Ignition method (LOI), after homogenising the samples with a mill and combusting the  
210 organic matter for 4h at 500 °C (Heiri et al., 2001).

211

### 212 **2.4 Estimation of sediment-water and air-sea CH<sub>4</sub> and CO<sub>2</sub> flux**

213 The sediment-water CO<sub>2</sub> and CH<sub>4</sub> diffusive fluxes were calculated using Fick's first law:

$$214 \quad J = -\phi D_S \frac{dC}{dz} \quad (2)$$

215 where  $J$  is diffusive flux of CH<sub>4</sub> and DIC (μmol m<sup>-2</sup> d<sup>-1</sup>),  $\phi$  is the sediment porosity,  $D_S$  is the  
216 sediment diffusion coefficient (cm<sup>2</sup> s<sup>-1</sup>),  $C$  is the CH<sub>4</sub> concentration in porewater (μM) and  $z$

217 is the sediment depth (cm). The values of  $\frac{dC}{dz}$  were obtained from the slope of the linear  
 218 regressions where  $p < 0.05$ . The diffusion in sediment ( $D_S$ ) was adjusted to the diffusion in  
 219 seawater using sediment tortuosity based on  $D_S = \frac{D_{SW}}{\theta}$ , where the seawater diffusion  
 220 coefficient ( $D_{SW}$ ) for CH<sub>4</sub> and DIC seawater at 20°C was  $1.39 \times 10^{-9}$  and  $9.89 \times 10^{-10}$  (Lerman,  
 221 1979). Tortuosity ( $\theta$ ) was calculated from sediment porosity using  $\theta = 1 - \ln(\phi^2)$   
 222 (Boudreau, 1997; Lengier et al., 2021).

223

224 The air-sea CO<sub>2</sub> and CH<sub>4</sub> fluxes were determined by gradient of air-sea gas concentration,  
 225 gas solubility and gas transfer velocity (Equation 1).

$$226 \quad FCH_4 / FCO_2 = k k_0 (P_w - P_a) \quad (3)$$

227 where  $F$  is the CO<sub>2</sub> and CH<sub>4</sub> flux ( $\text{mmol m}^{-2} \text{d}^{-1}$ ),  $k$  represents gas transfer velocity ( $\text{m d}^{-1}$ ),  $k_0$   
 228 is the solubility coefficient ( $\text{mol kg}^{-1} \text{atm}^{-1}$ ), and  $P_w$  and  $P_a$  are the partial pressures ( $\mu\text{atm}$ ) of  
 229 CO<sub>2</sub> and CH<sub>4</sub> in water and air, respectively. The atmospheric partial pressures of CO<sub>2</sub> and  
 230 CH<sub>4</sub> were 419 and 1.9 ppm, respectively. Positive air-sea gas flux values indicate gas evasion  
 231 from water to air. Four empirical models were used to determine the gas transfer velocity  $k$ ,  
 232 which was based on the water depth and wind speed at 10 m above sea level ( $\text{m s}^{-1}$ ) (Borges  
 233 et al., 2004; Dobashi & Ho, 2022; Raymond & Cole, 2001; Wanninkhof, 2014) (Table 1).  
 234 These models were selected for intermediate wind speed of 3–15  $\text{m s}^{-1}$ . Dobashi and Ho  
 235 (2022) model was determined in seagrass in Florida Bay, which accounted for the wave  
 236 resistance by seagrass and lower wind fetch in meadows. Dobashi and Ho (2022) model for  
 237 the analysis as it is more suitable for our coastal bay and prevents overestimation of fluxes.

238 **Table 1.** Models for gas transfer velocity parameterizations.  $k$  is normalized to Schmidt  
 239 number ( $k_{600}$ ) as a function of temperature and salinity.

Model	Parameters	Location	Equation
Raymond & Cole (2001)	Wind speed	River and estuary	$k_{600} = 1.91e^{0.35u_{10}}$
Borges et al., (2004)	Wind speed	Estuary	$k_{600} = 5.141u_{10}^{0.758}$
Wanninkhof (2014)*	Wind speed	River	$k_{660} = 0.251u_{10}^2$
Dobashi and Ho (2022)	Wind speed	Seagrass	$k_{600} = 0.125u_{10}^2$

240 *Note.*  $u_{10}$  is the wind speed at 10 m height ( $\text{m s}^{-1}$ ). \* $k_{660}$  is converted to  $k_{600}$  for comparison by  
 241 assuming that both the Schmidt number had the same ratio and exponent of -0.5.

242 To evaluate the global warming potential, CH<sub>4</sub> flux was converted to CO<sub>2</sub> equivalents. CH<sub>4</sub>  
 243 flux estimates were based on the sustained-flux global warming potential (SGWP) 96 and 45  
 244 for time horizons of 20 and 100 years, respectively (Al-Haj & Fulweiler, 2020; Neubauer &  
 245 Megonigal, 2015). The CO<sub>2</sub> equivalent emissions of CH<sub>4</sub> were calculated as follows:

$$246 \quad SGWP_{100/20}(Tg \text{ CO}_{2-eq}) = FCH_4 * 365 * A * SGWP_{100/20} * f \quad (5)$$

247 where  $FCH_4$  represents average CH<sub>4</sub> flux ( $\mu\text{mol m}^{-2} \text{d}^{-1}$ );  $A$  is the area of seagrass ( $\text{km}^2$ ),  
 248 SGWP of 100 and 20 years of 45 and 96,  $f$  is the conversion factor from  $\mu\text{mol}$  to Tg

249 To investigate whether CO<sub>2</sub> and CH<sub>4</sub> fluxes were different between stations, Mann-Whitney  
250 tests were used due to the non-normal distributed data. Spearman's Rank-order test was used  
251 to determine the correlations between different environmental parameters. All statistical tests  
252 were considered significant when  $p < 0.05$ .

253

## 254 **3 Results**

### 255 **3.1 Timeseries observations**

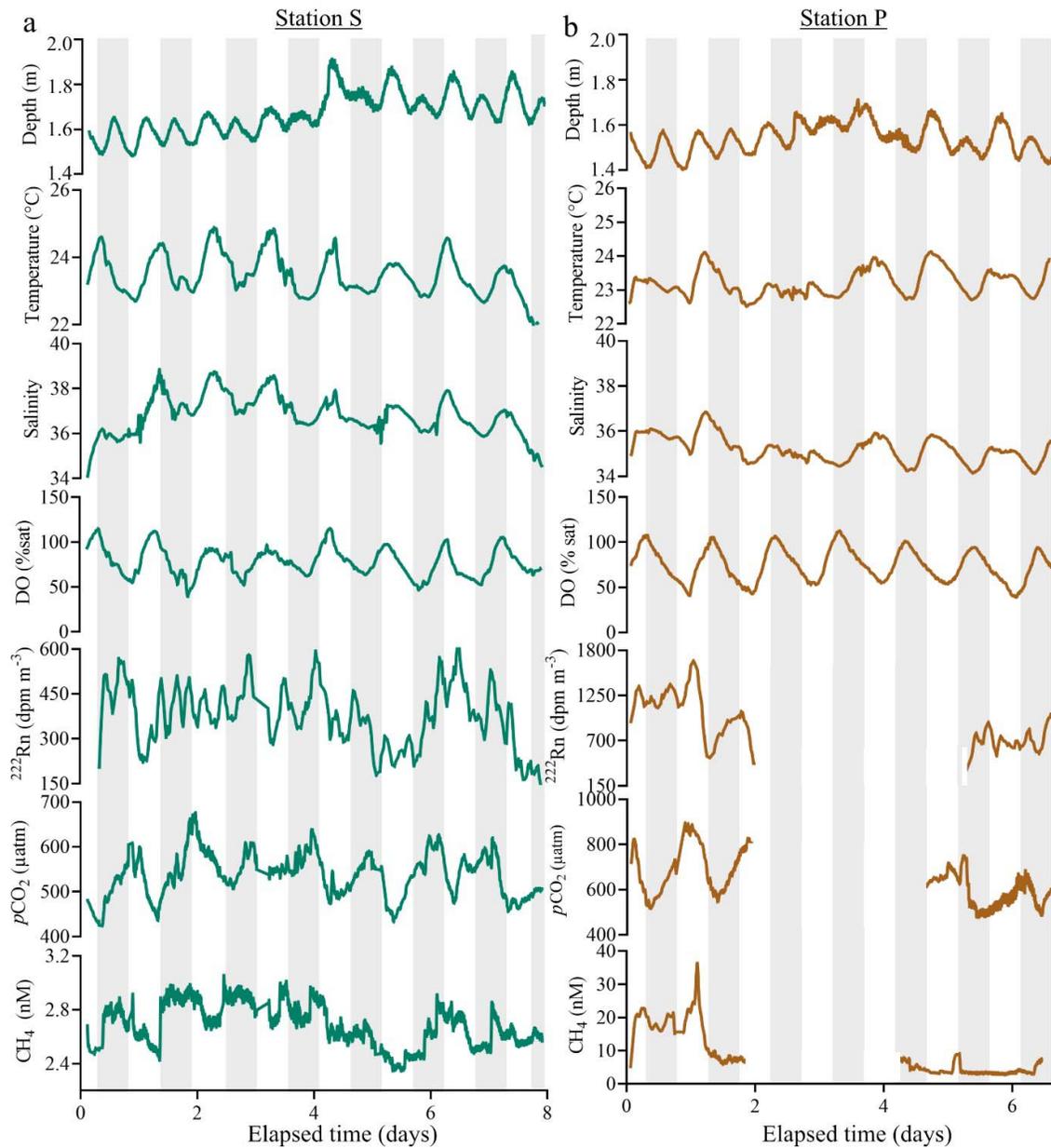
256 The average water temperature and salinity were similar at Stations S and P, with  $23.3 \pm 0.7$   
257 °C (SD) and  $36 \pm 1$  respectively (Figure 2). The water depth ranged from 1.4 to 2.4 m and  
258 wind speeds at 10 m above sea level averaged  $2.1 \pm 1.6 \text{ m s}^{-1}$  over the study period. The light  
259 intensity under the water was higher in Station P ( $1747 \pm 633 \text{ lum ft}^{-2}$ ) than Station S ( $1044 \pm$   
260  $670 \text{ lum ft}^{-2}$ ). Over diel periods, DO at both Stations S and P was undersaturated ( $77.9 \pm$   
261  $16.0\%$  and  $74.7 \pm 18.2\%$ , respectively). DO followed the expected diel pattern with  
262 oversaturated and undersaturated conditions during noon and night, respectively.  $p\text{CO}_2$   
263 exhibited a diel cycle with a peak around 9 to 10 am and lowest values around 6 pm and was  
264 negatively correlated with DO in both stations (Figure 2). The hourly average CH<sub>4</sub>  
265 concentrations were significantly different at both sites, with Station P were 5 times higher  
266 than Station S. We observed a 40% decrease in CH<sub>4</sub> concentrations from 11:00 to 14:00 at  
267 Station P, but only 6% decrease in Station P during noon in Station S. The daytime average  
268 wind speed, and the CH<sub>4</sub> and CO<sub>2</sub> fluxes were higher than at nighttime (Table 2). The hourly  
269 average of  $p\text{CO}_2$  exhibited a clockwise hysteresis loop with DO saturation and CH<sub>4</sub> at both  
270 sites and both stations exhibited a weak but significant correlation between DO saturation and  
271 CH<sub>4</sub> (Figure 7). The hourly average CH<sub>4</sub> concentration had a hysteretic pattern to light  
272 intensity in Station S but a strong correlation in Station P. However, <sup>222</sup>Rn did not follow a  
273 diel pattern at both stations.

### 274 **3.2 Spatial variation**

275  $p\text{CO}_2$  and CH<sub>4</sub> were significantly different between the two stations (Figure 6).  $p\text{CO}_2$  values  
276 at Station S ( $538 \pm 50 \text{ } \mu\text{atm}$ ), which is surrounded by healthy seagrass meadows, were lower  
277 than at Station P ( $632 \pm 103 \text{ } \mu\text{atm}$ ), which is mostly surrounded by dead *matte* and organic  
278 matter debris over sand (Table 2). Similarly, the CH<sub>4</sub> concentrations were five times lower in  
279 Station S ( $2.68 \pm 0.17 \text{ nM}$ ) compared to Station P ( $8.57 \pm 6.72 \text{ nM}$ ). <sup>222</sup>Rn concentration at  
280 Station P ( $383 \pm 125 \text{ dpm m}^3$ ) was also significantly lower than Station S ( $892 \pm 331 \text{ dpm}$   
281  $\text{m}^3$ ) (Figure 2). The high CH<sub>4</sub> concentrations at Station P (peak at  $36.3 \text{ nM}$  at 13:00) occurred  
282 in the first two days of observations coinciding with the high concentrations of <sup>222</sup>Rn (peak at  
283  $1886 \text{ dpm m}^3$ ) and high irradiance ( $6000 \text{ lum ft}^{-2}$ ) (Figure 3). <sup>222</sup>Rn concentrations were  
284 positively correlated with CH<sub>4</sub> at Station P ( $r = 0.73$ ) and Station S ( $r = 0.51$ ) and  $p\text{CO}_2$  ( $r =$   
285  $0.49$  and  $r = 0.32$ , respectively) (Figure 6). Net CH<sub>4</sub> emissions were observed in both stations,  
286 with one order of magnitude higher CH<sub>4</sub> sea-air fluxes at Station P ( $1.10 \pm 2.29 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ )  
287 compared to Station S ( $0.10 \pm 0.12 \text{ } \mu\text{mol m}^{-2} \text{ d}^{-1}$ ) over the study period. Similarly, net release  
288 of CO<sub>2</sub> to the atmosphere was up to 2-fold lower in Station S ( $3.75 \pm 2.63 \text{ mmol m}^{-2} \text{ d}^{-1}$ )  
289 compared to Station P ( $6.32 \pm 5.59 \text{ mmol m}^{-2} \text{ d}^{-1}$ ).

290 The CH<sub>4</sub> and CO<sub>2</sub> emissions were calculated from four different gas transfer models. CH<sub>4</sub>  
291 emissions estimated from Dobashi and Ho (2022) were 2-times, 6-times and 11-times smaller

292 than those obtained with the other gas transfer models tested: Wanninkhof (2014), Raymond  
293 & Cole (2001) and Borges et al., (2004), respectively.



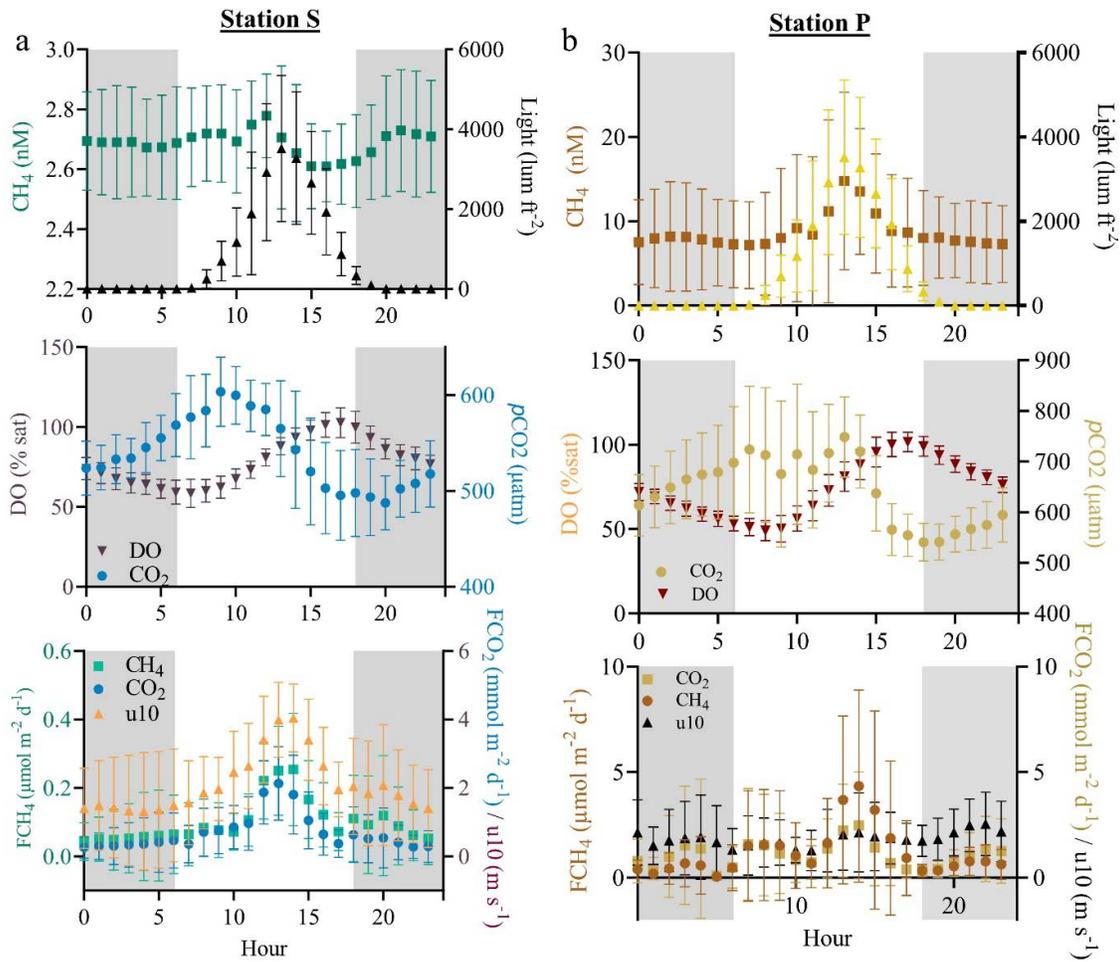
294

295 **Figure 2.** Timeseries observations of dissolved greenhouse gases and ancillary parameters at  
296 (a) Station S; and (b) Station P. The shaded area indicates nighttime, whereas the non-shaded  
297 area indicates daytime. Gaps in the data were due to instrument failure.

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302 **Figure 3.** Mean ± standard deviation of hourly concentration of CH<sub>4</sub> (nM), CO<sub>2</sub> (*p*CO<sub>2</sub>), light  
 303 light intensity (lum ft<sup>-2</sup>), percentage saturation of dissolved oxygen (DO, % sat), wind speed at 10  
 304 m above sea level (u10), CO<sub>2</sub> fluxes (FCO<sub>2</sub>), and CH<sub>4</sub> fluxes (FCH<sub>4</sub>) at Station S (left) and  
 305 Station P (right) over the period of study. Both CO<sub>2</sub> and CH<sub>4</sub> fluxes were obtained based on  
 306 the gas transfer model from (Dobashi & Ho, 2022). The shaded area indicates nighttime,  
 307 whereas the non-shaded area indicates daytime.

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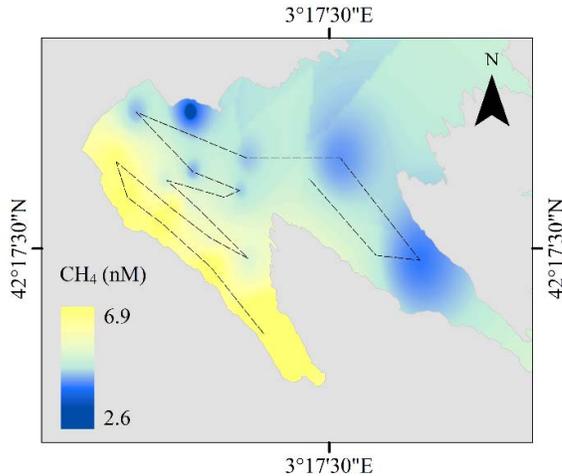
317 **Table 2.** A summary of environmental parameters and GHG fluxes measured simultaneously  
 318 at Station S and Station P. Day indicates data from 06:00 to 18:00 and night indicates data  
 319 from 18:00 to 06:00. All data are reported as mean  $\pm$  SD. The air-sea CO<sub>2</sub> and CH<sub>4</sub> fluxes  
 320 were calculated from four gas transfer velocity models (R&C from Raymond and Cole 2001;  
 321 B04 from Borges et al. 2004; W14 from Wanninkhof 2014; and RY22 from Dobashi and Ho  
 322 2022).

Description	Unit	Station S			Station P			Spatial Survey
		Overall	Day	Night	Overall	Day	Night	Overall
		<i>P.oceanica</i> dominated			Pachy and dead <i>P.oceanica</i>			Whole bay
No. of hours	hr	205	97	108	109	61	48	2
Temperature	°C	23.5 $\pm$ 0.6	23.0 $\pm$ 0.4	23.0 $\pm$ 0.3	23.2 $\pm$ 0.4	23.1 $\pm$ 0.1	23.3 $\pm$ 0.1	23.7*
Salinity		36.8 $\pm$ 0.9	37 $\pm$ 1	37 $\pm$ 1	36 $\pm$ 1	35 $\pm$ 0	35 $\pm$ 0	37 $\pm$ 0*
Water depth	m	1.7 $\pm$ 0.1	1.7 $\pm$ 1	1.7 $\pm$ 1	1.5 $\pm$ 0.1	1.5 $\pm$ 0.1	1.5 $\pm$ 0.1	1.7*
Wind speed	m s <sup>-1</sup>	2.6 $\pm$ 1.6	2.6 $\pm$ 1.1	1.6 $\pm$ 1.4	1.8 $\pm$ 1.4	1.7 $\pm$ 0.4	1.9 $\pm$ 0.4	1.6 $\pm$ 0.1*
Irridance	lum ft <sup>-2</sup>	526 $\pm$ 942	1044 $\pm$ 670	18 $\pm$ 0	873 $\pm$ 1456	1747 $\pm$ 633	33 $\pm$ 70	/
DO	% Sat	78 $\pm$ 16	79 $\pm$ 6.8	76 $\pm$ 6.5	75 $\pm$ 18	74 $\pm$ 1	74 $\pm$ 1	102 $\pm$ 1*
DO	mg L <sup>-1</sup>	5.4 $\pm$ 1.1	5.4 $\pm$ 0.5	5.2 $\pm$ 0.4	5.0 $\pm$ 1.3	4.5 $\pm$ 0.5	5.5 $\pm$ 0.4	7 $\pm$ 0*
pCO <sub>2</sub>	μatm	538 $\pm$ 50	561 $\pm$ 41	522 $\pm$ 27	632 $\pm$ 103	677 $\pm$ 36	614 $\pm$ 20	606 $\pm$ 51
CH <sub>4</sub>	nM	2.68 $\pm$ 0.17	2.69 $\pm$ 0.17	2.69 $\pm$ 0.19	8.57 $\pm$ 6.72	9.82 $\pm$ 1.83	7.72 $\pm$ 0.72	4.07 $\pm$ 1.18
<sup>222</sup> Rn	dpm m <sup>-3</sup>	377 $\pm$ 129	392 $\pm$ 159	376 $\pm$ 130	892 $\pm$ 331	863 $\pm$ 128	933 $\pm$ 81	/
<b>CO<sub>2</sub> flux</b>								
R&C	mmol m <sup>-2</sup> d <sup>-1</sup>	3.75 $\pm$ 2.63	5.12 $\pm$ 2.44	2.81 $\pm$ 1.59	6.32 $\pm$ 5.59	7.88 $\pm$ 2.27	5.53 $\pm$ 2.8	4.21 $\pm$ 0.84
B04	mmol m <sup>-2</sup> d <sup>-1</sup>	7.22 $\pm$ 5.27	10.36 $\pm$ 4.7	4.91 $\pm$ 2.97	11.85 $\pm$ 11.05	15.19 $\pm$ 4.79	9.96 $\pm$ 3.6	9.52 $\pm$ 2.01
W14	mmol m <sup>-2</sup> d <sup>-1</sup>	1.35 $\pm$ 1.78	2.10 $\pm$ 1.69	0.82 $\pm$ 1.21	2.13 $\pm$ 3.58	2.77 $\pm$ 1.6	1.75 $\pm$ 2.15	0.85 $\pm$ 0.20
RY22	mmol m <sup>-2</sup> d <sup>-1</sup>	0.64 $\pm$ 0.85	1.00 $\pm$ 0.76	0.39 $\pm$ 0.57	1.01 $\pm$ 1.70	1.31 $\pm$ 0.76	0.83 $\pm$ 1.02	0.38 $\pm$ 0.09
<b>CH<sub>4</sub> flux</b>								
R&C	μmol m <sup>-2</sup> d <sup>-1</sup>	0.56 $\pm$ 0.37	0.66 $\pm$ 0.36	0.49 $\pm$ 0.31	6.59 $\pm$ 9.21	9.76 $\pm$ 3.18	4.37 $\pm$ 0.80	1.33 $\pm$ 0.65
B04	μmol m <sup>-2</sup> d <sup>-1</sup>	1.07 $\pm$ 0.71	1.32 $\pm$ 0.66	0.87 $\pm$ 0.58	12.71 $\pm$ 18.73	19.71 $\pm$ 5.74	7.75 $\pm$ 1.59	2.97 $\pm$ 1.47
W14	μmol m <sup>-2</sup> d <sup>-1</sup>	0.20 $\pm$ 0.26	0.28 $\pm$ 0.24	0.15 $\pm$ 0.21	2.34 $\pm$ 4.88	4.24 $\pm$ 2.59	1.01 $\pm$ 0.83	0.27 $\pm$ 0.14
RY22	μmol m <sup>-2</sup> d <sup>-1</sup>	0.10 $\pm$ 0.12	0.13 $\pm$ 0.1	0.07 $\pm$ 0.1	1.10 $\pm$ 2.29	2.00 $\pm$ 1.21	0.48 $\pm$ 0.39	0.12 $\pm$ 0.10

323

### 324 3.3 Spatial survey in the bay

325 The 2-hour survey across the bay was conducted in late afternoon with wind speed (1.6 m s<sup>-1</sup>)  
 326 lower than the average timeseries measurements (2.2 m s<sup>-1</sup>). CH<sub>4</sub> concentrations varied across  
 327 the bay, ranging from 2.6 to 6.9 nM. The highest CH<sub>4</sub> concentration was detected around  
 328 Station P and along the SW shoreline, and further decreased towards the east and the opening  
 329 towards the Mediterranean Sea (Figure 4). This trend is consistent with timeseries  
 330 observations. Overall, a net release of CH<sub>4</sub> was estimated for the whole bay, ranging from  
 331 0.12  $\pm$  0.10 to 2.97  $\pm$  1.47 μmol m<sup>-2</sup> d<sup>-1</sup>, depending on the gas transfer model used. The  
 332 spatial survey represents the average of whole bay (0.21 km<sup>2</sup>), which was 50% higher than  
 333 the average timeseries measurements recorded at Station S and 91% lower at Station P. For  
 334 the upscaling of CH<sub>4</sub> emissions, we used the average CH<sub>4</sub> flux for the whole bay to account  
 335 for the spatial differences.

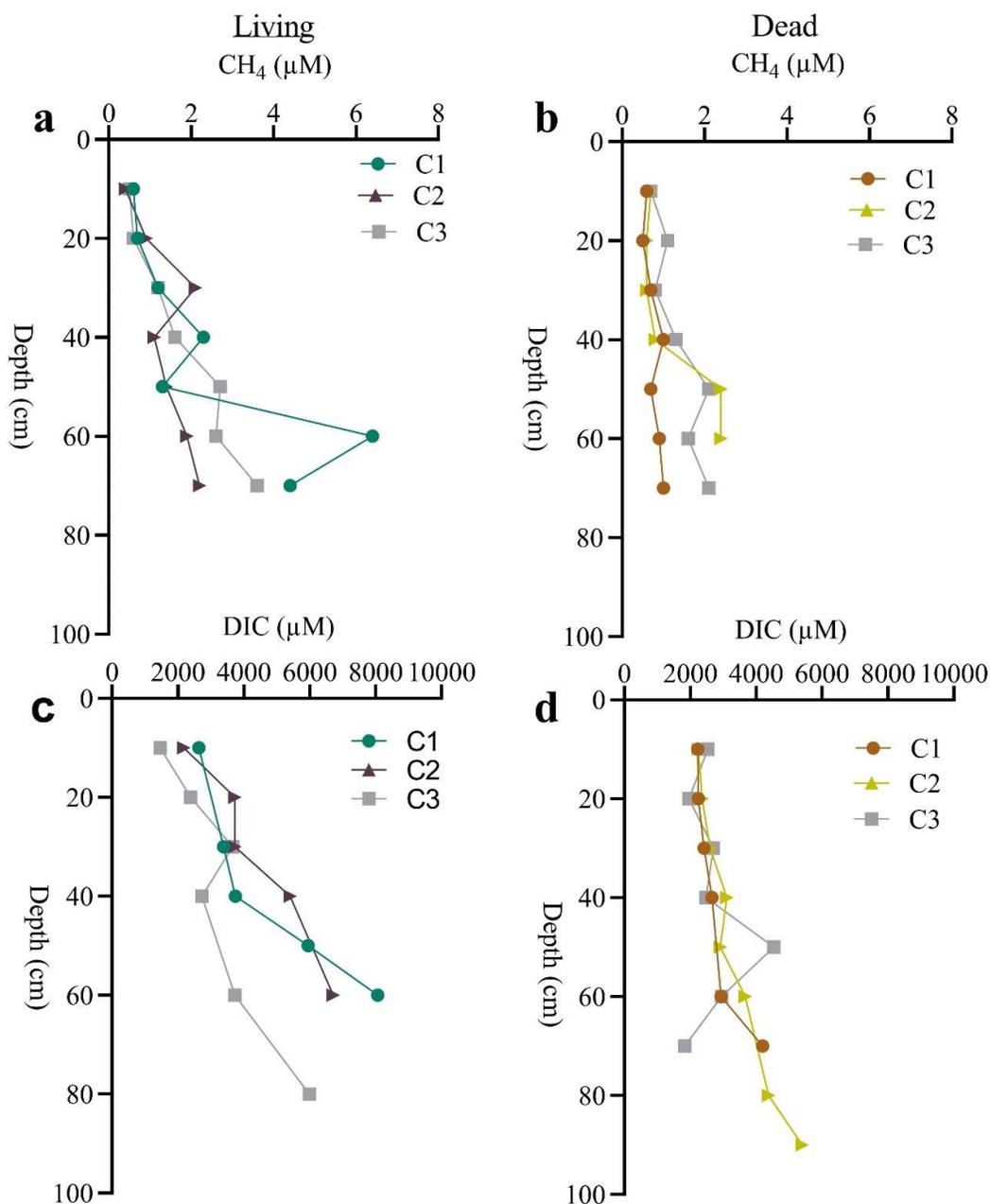


336

337 **Figure 4.** The distribution of CH<sub>4</sub> concentration across Portlligat bay. The dashed black line  
 338 represents the spatial survey. The northeast exit of the bay is the Mediterranean Sea.

339 **3.4 Porewater profiles**

340 Sediment cores in both living and dead seagrass areas had similar water content ranging from  
 341 40% to 55%. Total organic matter content of sediments was similar between cores from  
 342 living and dead seagrass areas, with an average of 37.9% and 44.3%, respectively (Table 3).  
 343 Porewater CH<sub>4</sub> concentration in living seagrass cores were two-times higher than in the dead  
 344 seagrass. Both cores showed similar CH<sub>4</sub> depth profiles, increasing from 1 μM at the surface  
 345 up to 6 μM at 50 cm (Figure 5). The estimated sediment diffusive CH<sub>4</sub> flux in living seagrass  
 346 (0.1 – 0.4 μmol m<sup>-2</sup> d<sup>-1</sup>) was 2 to 11 times higher than in dead seagrass (0 – 0.1 μmol m<sup>-2</sup> d<sup>-1</sup>).  
 347 CH<sub>4</sub> sediment-water fluxes in the living seagrass were 2.5 times higher than CH<sub>4</sub> air-sea  
 348 emissions in the Station S (i.e., seagrass-dominated site), whereas sediment-water CH<sub>4</sub> fluxes  
 349 in the dead seagrass were 0.1 times lower than air-sea emissions in Station P (i.e., a mix of  
 350 patchy and dead seagrass). Porewater DIC concentrations in living seagrass (1,460 to 8,060  
 351 μM) were also two times higher than in the dead seagrass (940 to 5,390 μM) (Table 3). DIC  
 352 concentration in dead seagrass remained relatively constant with increasing sediment depth,  
 353 whilst in living seagrass increased steeply up to 30 cm, where the rhizosphere ends, and then  
 354 after continued to increase until 70 cm depth (Figure 5). The estimated DIC diffusive flux in  
 355 the living seagrass (185 – 355 μmol m<sup>-2</sup> d<sup>-1</sup>) was three-times higher than in the dead seagrass  
 356 (68 – 88 μmol m<sup>-2</sup> d<sup>-1</sup>).



357

358 **Figure 5.** Vertical sediment profiles of porewater CH<sub>4</sub> concentrations (µM) in three replicate  
 359 cores within a) living meadows and b) dead mat; and DIC concentrations in c) living  
 360 meadows and d) dead mat.

361 **Table 3.** Sediment characteristics and porewater DIC and CH<sub>4</sub> concentrations in 50cm thick  
 362 cores from living meadows and dead mat cores. All data are reported as mean ± SD.

	Unit	Living	Dead
Dry Bulk density <sup>a</sup>	g cm <sup>-3</sup>	0.2 ± 0.1	0.3 ± 0.1
Water content <sup>a</sup>	%	51 ± 5.1	46 ± 4.9
Particulate Organic matter <sup>a</sup>	%	16.9 ± 7.4	17.5 ± 7.4

DIC	$\mu\text{M}$	4094 $\pm$ 1827	2974 $\pm$ 939
CH <sub>4</sub>	$\mu\text{M}$	2.3 $\pm$ 1.5	1.1 $\pm$ 0.6
CH <sub>4</sub> sediment-water flux	$\mu\text{mol m}^{-2} \text{d}^{-1}$	0.25 $\pm$ 0.1	0.1 $\pm$ 0.1
DIC sediment-water flux	$\mu\text{mol m}^{-2} \text{d}^{-1}$	280 $\pm$ 87	78 $\pm$ 15

363 <sup>a</sup>Average of the first 50 cm of the sediment

364

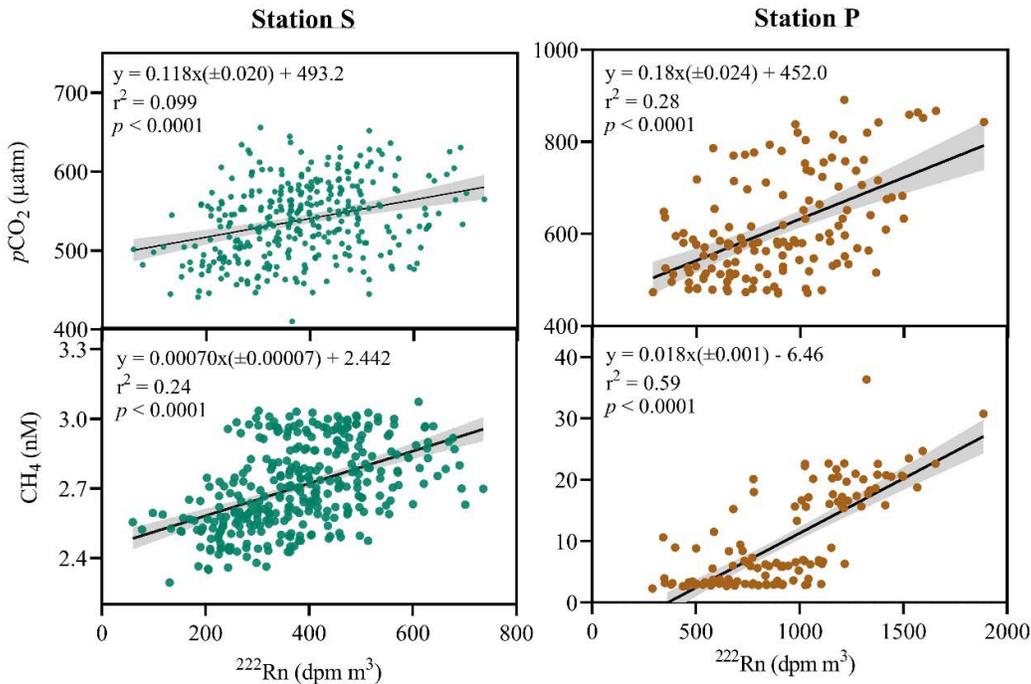
## 365 4 Discussion

### 366 4.1 Porewater methane fluxes

367 Organic sediments in anoxic conditions support methanogenic activity and can result in high  
368 carbon mineralization rates and thus benthic CH<sub>4</sub> effluxes. The high porewater CH<sub>4</sub>  
369 concentration (0.3 – 2.1  $\mu\text{M}$ ) in both living and dead seagrass sediment, was 20 times higher  
370 than previously measured in Italy for the same seagrass species (0.04–0.09  $\mu\text{M}$ ), but similar  
371 to those estimated for *Zostera noltii* in France (2.5 – 8  $\mu\text{M}$ ) (Deborde et al., 2010; Schorn et  
372 al., 2022). This might be related to abiotic factors including sediment grain-size distribution  
373 (i.e., mud content), and/or the quality and quantity of organic carbon in sediment. The higher  
374 CH<sub>4</sub> production below 40 – 50 cm sediments in seagrass sediments compared to the relative  
375 flat CH<sub>4</sub> trend in the dead matte could be related to the effects of oxygen pumping by the  
376 seagrass rhizosphere on methanogenic activity (Figure 5). The CH<sub>4</sub> consumption could occur  
377 in upper layer (Schorn et al., 2022). Positive correlations between the porewater tracer <sup>222</sup>Rn  
378 and CH<sub>4</sub> concentrations also suggested that the sediments underlying the seagrasses are the  
379 main source of CH<sub>4</sub> (and <sup>222</sup>Rn) into the environment (Figure 6). There are no other major  
380 <sup>222</sup>Rn sources such as fresh groundwater or river water input to the bay. Higher sediment-  
381 water fluxes than the air-sea water fluxes in dense seagrass (Station S) also implied that the  
382 sediment is the source.

383 High organic carbon in sediments support CH<sub>4</sub> production. A positive relationship between  
384 porewater DIC and CH<sub>4</sub> concentrations suggested that methanogenesis supports organic  
385 carbon mineralization (Aleksandra & Katarzyna, 2018). Both DIC and CH<sub>4</sub> diffusion rates in  
386 the living seagrass were 2–3 times higher than in sediments of dead seagrasses, suggesting  
387 that living seagrass releases organic carbon together with O<sub>2</sub> in root exudates, which enhances  
388 carbon remineralization rates and thus DIC fluxes (Li, 2021). Living seagrasses, with a higher  
389 liable content of labile organic carbon compared to dead *matte* could stimulate the CH<sub>4</sub>  
390 production (Piñeiro-Juncal et al., 2021), which was also observed in sediments with *Z. noltii*,  
391 which had four-times higher fluxes than bare sediments (Bahlmann et al., 2015). However,  
392 based on the sediment CH<sub>4</sub>: DIC, the contribution of methanogenesis to total carbon  
393 mineralization was at maximum 0.03%.

394 Our CH<sub>4</sub> diffusive sediment-water flux in living and dead *P. oceanica* of (0.2  $\mu\text{mol m}^{-2} \text{d}^{-1}$  and  
395 0.08  $\mu\text{mol m}^{-2} \text{d}^{-1}$ , respectively) at Portlligat Bay was 2 orders of magnitude lower than the  
396 fluxes measured in Fetoviaia Bay (median of 106  $\mu\text{mol m}^{-2} \text{d}^{-1}$  living; 142  $\mu\text{mol m}^{-2} \text{d}^{-1}$  for  
397 dead) (Schorn et al., 2022), using core incubations. While the flux may not be directly  
398 comparable due to different methods, both studies supported the hypothesis that dead  
399 *P. oceanica* could accumulate CH<sub>4</sub> due to the production of methylated compounds that fuels  
400 methanogenesis (Schorn et al. 2022).



401

402 **Figure 6.** Scatter plot of  $^{222}\text{Rn}$  against  $\text{CH}_4$  and  $p\text{CO}_2$  in Station S (left) and Station P (right).  
 403 The solid line represents the fitted regression equation, the shaded area are the 95%  
 404 confidence limits of the regression line, the  $r^2$  value the degree of correlation, and the  $p$  value  
 405 the level of significance.

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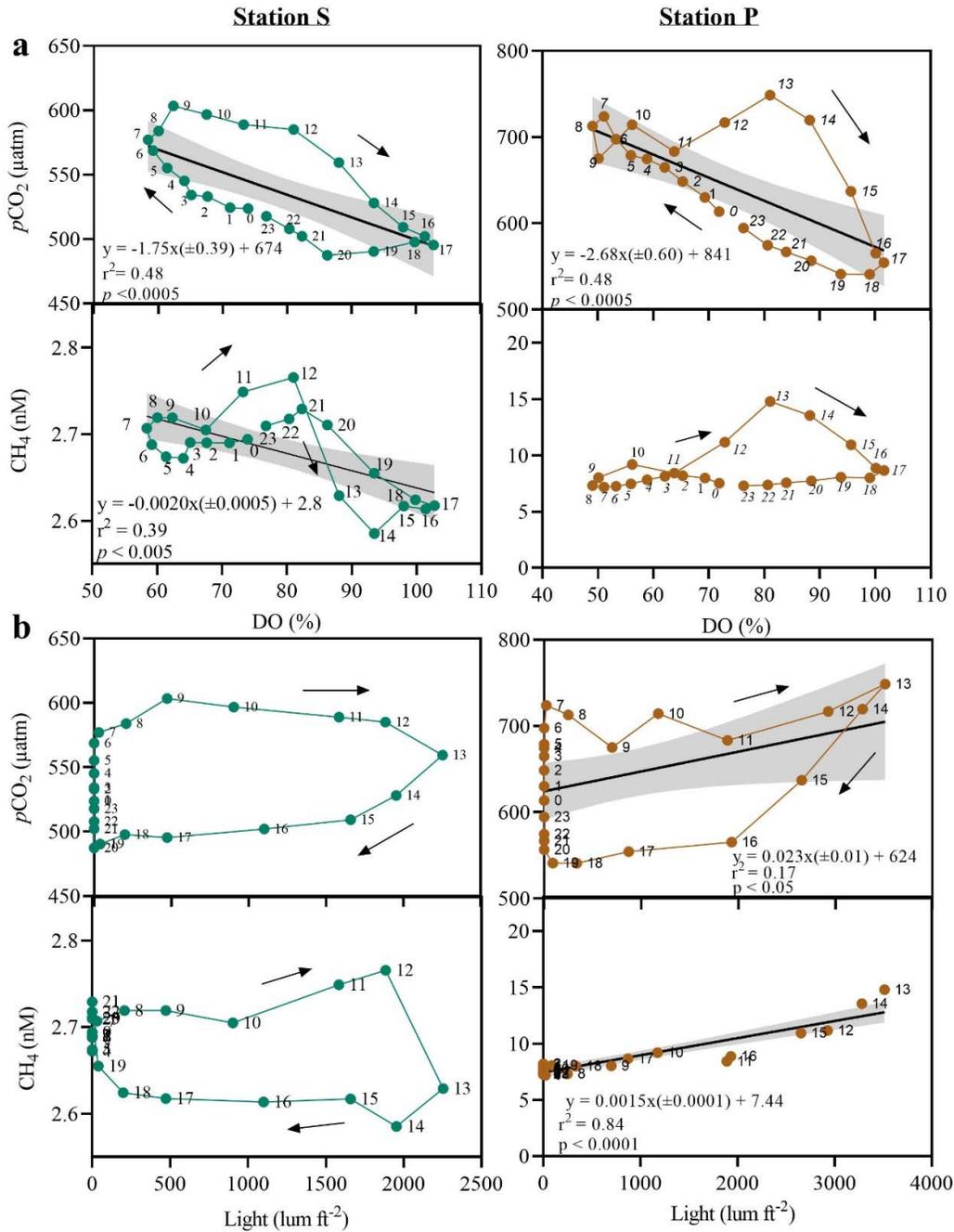
#### 407 4.2 Diel pattern in air-sea fluxes of $\text{CH}_4$

408 A diel air-sea  $\text{CH}_4$  pattern with a decreasing trend in afternoon suggests that oxygen  
 409 availability can control  $\text{CH}_4$  emissions to the atmosphere (Figure 3). A 6% to 40% decrease  
 410 of  $\text{CH}_4$  concentrations in the afternoon coinciding with increasing DO and high light intensity  
 411 indicates higher  $\text{CH}_4$  oxidation rate within the water column due to higher oxygen  
 412 concentration derived from seagrass photosynthesis (Bahlmann et al., 2015) (Figure 7).  
 413 Increased oxygen from the roots or plant could stimulate aerobic  $\text{CH}_4$  oxidation in the water  
 414 column (Al-Haj & Fulweiler, 2020). Similarly, Lyimo et al., (2018) reported that a reduction  
 415 of photosynthetic activity result in an increase of  $\text{CH}_4$  emissions in a tropical seagrass  
 416 meadow. Lower air-sea  $\text{CH}_4$  emissions in the dense seagrass site (Station S) further  
 417 demonstrates that photosynthesis could limit  $\text{CH}_4$  emissions. The diel  $\text{CH}_4$  variation likely  
 418 implied that the productivity of seagrass drives the oxidation rate of  $\text{CH}_4$ , controlling  $\text{CH}_4$   
 419 emissions.

420 The patchy seagrass contributed to a higher  $\text{CH}_4$  flux than the dense seagrass and exhibited a  
 421 more pronounced  $\text{CH}_4$  peak during noon, which was not observed in the dense seagrass. This  
 422  $\text{CH}_4$  peak could be produced during photosynthesis of submerged photosynthetic organisms  
 423 as ebullition or through direct  $\text{CH}_4$  production, including seagrass, cyanobacteria and algae  
 424 during (Hilt et al., 2022). The positive correlation of light intensity with  $\text{CH}_4$  concentrations  
 425 observed only in patchy seagrass might suggest abiotic  $\text{CH}_4$  photoproduction (Figure 7). A

426 peak of CH<sub>4</sub> towards noon was also observed in other submerged vegetated habitats such as  
427 temperate freshwater marsh in China and a mixed-vegetated habitat in a nearshore bay in the  
428 Baltic Sea during summer (Ding et al., 2004; Roth et al., 2022). Moreover, the dead seagrass  
429 debris could serve as a source of methylated compounds and stimulate the CH<sub>4</sub> production  
430 (Schorn et al., 2022). More studies are needed to understand the contribution of both seagrass  
431 meadows and dead matte habitat to CH<sub>4</sub> production.

432 The high spatial differences in CH<sub>4</sub> concentrations could link to the proximity to the open  
433 ocean. The patchy seagrass area had two-times higher <sup>222</sup>Rn concentrations and ten-times  
434 greater CH<sub>4</sub> fluxes than the area with dense seagrass. As the dense seagrass site was closer to  
435 the open ocean, ocean waters could dilute CH<sub>4</sub> concentration within the area, resulting in a  
436 lower CH<sub>4</sub> and <sup>222</sup>Rn concentrations compared to the more enclosed location of Station P  
437 with patchy seagrass (Rosentreter, Borges, et al., 2021).



438

439 **Figure 7.** a) Scatter plot of average hourly values of dissolved oxygen (DO) and b) and light  
 440 intensity against  $\text{CH}_4$  and  $\text{CO}_2$  in Station S (left) and Station P (right). The solid line  
 441 represents the fitted regression equation ( $\pm\text{SE}$ ), and the shaded area are the 95% confidence  
 442 limits of the regression line, the  $r^2$  value the degree of correlation, and the  $p$  value the level of  
 443 significance. The numbers inside the plots indicate the hour of the day. Arrows indicates the  
 444 hysteresis pattern along the day.

445

446

### 447 **4.3 Low seagrass CH<sub>4</sub> emissions on local and global scales**

448 The average air-sea CH<sub>4</sub> flux ( $0.12 \pm 0.10 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) estimated are the lowest among  
449 seagrass meadows reported to date, which can reach up to  $307 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$  (Table 4).  
450 Our fluxes using the seagrass-derived *k* model from Dobashi and Ho (2022) were 2-11 times  
451 lower than other *k* models often used for coastal or open ocean (Borges et al., 2004; Raymond  
452 & Cole, 2001; Wanninkhof, 2014). Seagrass meadows attenuate wave energy compared to  
453 bare sediment. Therefore, using coastal ocean gas transfer *k* models might overestimate the  
454 CH<sub>4</sub> emissions (Table 2). For example, Ollivier et al. (2022) and Banerjee et al. (2018) applied  
455 B04 and W14 models, respectively, which partially explains their higher CH<sub>4</sub> emissions.

456 Another reason for our relatively low CH<sub>4</sub> flux could be the lack of other freshwater sources  
457 at our study site. Methane-enriched freshwater inputs could result in overestimates of CH<sub>4</sub>  
458 fluxes within seagrass meadows. The air-water CH<sub>4</sub> fluxes from our sites and Australia  
459 (Ollivier et al., 2022) ( $10.6 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) were at the lower end of published data (Table  
460 4). Both studies were located in coastal bays with high salinity and limited tidal or freshwater  
461 influence. Our fluxes were two orders of magnitude lower than a brackish lagoon in India  
462 ( $120 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ), and a meso-tidally lagoon in Portugal ( $307 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ),  
463 France and US (Table 4) (Al-Haj et al., 2022; Bahlmann et al., 2015; Banerjee et al., 2018).  
464 These other seagrass sites were in tidal systems with freshwater inputs suggesting that the  
465 reported high CH<sub>4</sub> fluxes could be partially explained by external freshwater or marsh inputs.  
466 This has been observed in other tidally-influenced ecosystems such as mangroves and  
467 saltmarshes where higher CH<sub>4</sub> concentration in porewater drives the high surface water CH<sub>4</sub>  
468 (Call et al., 2018; Santos et al., 2019; Yau et al., 2022). Flanking saltmarshes adjacent to  
469 seagrass export CH<sub>4</sub>, elevating CH<sub>4</sub> flux in the seagrass meadows (Al-Haj et al., 2022). Since  
470 our system is not directly influenced by flanking marshes, porewater, and freshwater inputs,  
471 the relatively low CH<sub>4</sub> air-sea fluxes likely represent emissions from subtidal seagrass  
472 habitats.

473 We combined our results with the literature to re-evaluate global CH<sub>4</sub> emissions from  
474 seagrass meadows. It is important to differentiate between sediment-water and air-sea fluxes  
475 (Table 4). Fluxes from benthic chamber and sediment core incubation only capture the CH<sub>4</sub>  
476 from the sediment to water but do not account for the exchange of CH<sub>4</sub> across the water-air  
477 interface or potentially CH<sub>4</sub> oxidation in the water column (Asplund et al., 2022; Bonaglia et  
478 al., 2017; Schorn et al., 2022). Our sediment-water fluxes were up to 2 times higher than the  
479 air-sea CH<sub>4</sub> fluxes. Earlier global estimates of seagrass CH<sub>4</sub> emissions to the atmosphere  
480 ( $1.25$  to  $401 \mu\text{mol CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) were extrapolated from studies using benthic chambers and  
481 sediment core incubations (Rosentreter et al. (2021b)). Our results show that sediment-water  
482 fluxes do not necessarily represent water-air fluxes. Therefore, we updated earlier  
483 compilations (Al-Haj et al., 2022) to differentiate between air-sea (8 sites) and sediment-  
484 water CH<sub>4</sub> (20 sites) fluxes in seagrass meadows (Table 4). Both air-sea and sediment-water  
485 CH<sub>4</sub> fluxes are highly variable. The geometric mean of air-sea and sediment-water CH<sub>4</sub>  
486 fluxes ( $21.6$  and  $26.1 \mu\text{mol m}^{-2} \text{ d}^{-1}$ , respectively) was 3-fold lower than arithmetic mean  
487 values ( $61.6 \pm 19.4$  and  $81.0 \pm 19.8 \mu\text{mol m}^{-2} \text{ d}^{-1}$ , respectively). The skewed dataset suggests  
488 that geometric mean is likely a more realistic representation of fluxes (Williamson & Gattuso,  
489 2022). Overall, previous compilations may have overestimated CH<sub>4</sub> emissions by relying on  
490 sediment-water fluxes and mean values rather than air-sea and geometric mean values.

491 **Table 4.** Mean of methane (CH<sub>4</sub>) in air-sea and sediment-water fluxes in seagrass reported  
 492 in the literature. The mean (± SE), geometric mean and median of air-sea and sediment-water  
 493 CH<sub>4</sub> fluxes represent the global average.

Location	Species	CH <sub>4</sub> flux (μmol m <sup>-2</sup> d <sup>-1</sup> )	Site	Method
<i>Water-air</i>				
Chilika Lagoon, India <sup>1</sup>	<i>Halodule sp. and Halophila sp</i>	120.0	Tidal lagoon	Water samples
Arcachon Lagoon, France <sup>2</sup>	<i>Z. noltii</i>	42.0	Tidal lagoon	Discrete Water samples
Wallagoot, Australia <sup>3</sup>	<i>R. megacarpa</i>	33.8	Mouth of estuary	Continous surface water
East Harbor, Massachusetts, USA <sup>4</sup>	<i>Z. marina</i>	107.5	Lagoon + marsh	Discrete water samples
Pleasant Bay, Massachusetts, USA <sup>4</sup>	<i>Z. marina</i>	113.8	Coastal lagoon	Discrete water samples
Swan Bay, Australia <sup>5</sup>	<i>Z. mulleri</i>	10.6	Tidal lagoon	Continous surface water
Cadaques, Spain <sup>6</sup>	<i>P. oceanica</i>	0.1	Coastal bay	Continous surface water
	<b>Mean</b>	<b>61.1 (± 19.4)</b>		
	<b>Geometric mean</b>	<b>21.6</b>		
	<b>Median</b>	<b>42.0</b>		
<i>Sediment-water</i>				
Florida, USA <sup>7</sup>	<i>T. testudinum</i>	44.0	Coastal lagoon	Benthic chamber
Bimini, Bahamas <sup>7</sup>	<i>S. filiforme</i>	5.8	Coastal bay	Benthic chamber
Moreton Bay, Australia <sup>8</sup>	<i>Z. capricorni</i>	348.0	Coastal lagoon	Core incubation
Florida, USA <sup>9</sup>	<i>T. testudinum</i>	183.4	Coastal lagoon	Benthic chamber
Tomales Bay, USA <sup>10</sup>	<i>Z. marina</i>	35.7	Coastal inlet	Benthic chamber
Awerange Bay, Indonesia <sup>11</sup>	<i>E. acoroides</i>	95.7	Coastal bay	Benthic chamber
Arcachon Lagoon, France <sup>2</sup>	<i>Z. noltii</i>	98.4	Tidal lagoon	Water samples
Ria Formosa Lagoon, Portugal <sup>12</sup>	<i>Z. noltii</i>	307.2	Tidal lagoon	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>H. uninervis</i>	48.1	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>C. serrulata and H. uninervis</i>	401.3	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>E. acoroides</i>	96.2	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>T. ciliatum</i>	3.2	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>H. decipiens</i>	1.4	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>T. hemprichii</i>	6.5	Coastal inlet	Core incubation
Red Sea, Saudi Arabia <sup>13</sup>	<i>H. stipulacea and H. uninervis</i>	61.0	Coastal inlet	Core incubation
Chwaka Bay, Tanzania <sup>14</sup>	<i>T. hemprichii</i>	74.8	Coastal bay + mangrove	Benthic chamber
Red Sea, Saudi Arabia <sup>15</sup>	<i>H. stipulacea and H. uninervis</i>	59.7	Coastal lagoon	Core incubation
Virginia, USA <sup>16</sup>	<i>Z. marina</i>	136.7	Coastal bay with marsh	Benthic chamber
Mediterranean Sea, Italy <sup>17</sup>	<i>P. oceanica</i>	106.0	Coastal bay	Core incubation
Wallis Lake, Australia <sup>3</sup>	<i>H. ovalis</i>	45.4	Mouth of estuary	Benthic chamber
Wallis Lake, Australia <sup>3</sup>	<i>P. australia</i>	279.3	Mouth of estuary	Benthic chamber
Wallis Lake, Australia <sup>3</sup>	<i>Z. muelleri</i>	46.0	Mouth of estuary	Benthic chamber
Wallis Lake, Australia <sup>3</sup>	<i>Z. muelleri</i>	10.9	Mouth of estuary	Benthic chamber
Finnland <sup>18</sup>	<i>Z. marina</i>	1.6	Coastal bay	Benthic chamber
Denmark <sup>18</sup>	<i>Z. marina</i>	3.4	Fjord and coastal bay	Benthic chamber
Sweden <sup>18</sup>	<i>Z. marina</i>	2.6	Coastal bay	Benthic chamber
East Harbor, Massachusetts, USA <sup>4</sup>	<i>Z. marina</i>	0.0	Back-barrier lagoon	Benthic chamber
Pleasant Bay, Massachusetts, USA <sup>4</sup>	<i>Z. marina</i>	73.3	Coastal lagoon	Benthic chamber
Cadaques, Spain <sup>6</sup>	<i>P. oceanica</i>	0.3	Coastal bay	Porewater samples
	<b>Mean</b>	<b>81.0 (± 19.8)</b>		
	<b>Geometric mean</b>	<b>26.1</b>		
	<b>Median</b>	<b>47.1</b>		

494

495 <sup>1</sup>Banerjee et al., 2018; <sup>2</sup>Deborde et al., 2010; <sup>3</sup>Camillini, 2020; <sup>4</sup>Al-Haj et al., 2022; <sup>5</sup>Ollivier  
 496 et al., 2022; <sup>6</sup>This study; <sup>7</sup>Oremland, 1975; <sup>8</sup>Moriarty et al., 1984; <sup>9</sup>Barber & Carlson, 1993;

497 <sup>10</sup>[Sansone et al., 1998](#); <sup>11</sup>[Alongi et al., 2008](#); <sup>12</sup>[Bahlmann et al., 2015](#); <sup>13</sup>[Garcias-Bonet, 2017](#);  
498 <sup>14</sup>[Lyimo et al., 2018](#); <sup>15</sup>[Burkholz et al., 2020](#); <sup>16</sup>[Oreska et al., 2020](#); <sup>17</sup>[Schorn et al., 2022](#); <sup>18</sup>

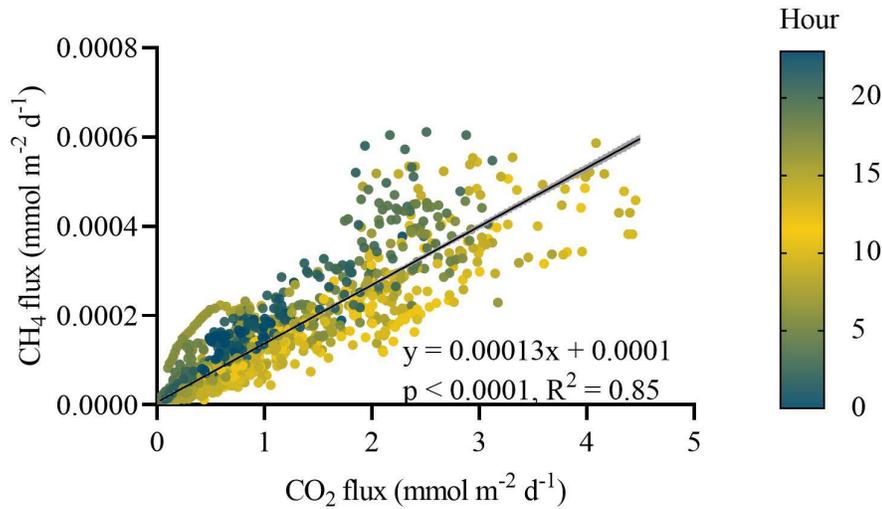
499 [Asplund et al., 2022](#)

#### 500 **4.4 Implications for net carbon sequestration**

501 To evaluate the global warming potential of CH<sub>4</sub> emissions in seagrass and the potential  
502 offset from carbon burial benefits, air-sea CH<sub>4</sub> fluxes were converted to CO<sub>2</sub>-equivalents in  
503 20 and 100 year time horizons using sustained-flux global warming potential (SGWP) of 96  
504 and 45, respectively (Neubauer & Megonigal, 2015). Using different metrics could change  
505 the interpretation of the global climatic impact of methane emissions. Our average CH<sub>4</sub> fluxes  
506 in Portilligat bay are equivalent to 0.05 and 0.03 g CO<sub>2</sub>-eq m<sup>2</sup> yr<sup>-1</sup> in 20 and 100 year time  
507 horizons, respectively. The carbon burial rates from seagrass meadows at our study site have  
508 been estimated at 142 ± 69 g C m<sup>-2</sup> yr<sup>-1</sup> (Serrano et al., 2016). Therefore, the estimated air-sea  
509 CH<sub>4</sub> emissions from *P. oceanica* in our site offset the carbon burial only by < 0.7 % in a 20-  
510 year time horizon. The low CH<sub>4</sub> offset is attributed to the low CH<sub>4</sub> flux and high carbon  
511 burial of *P. oceanica*. Our average CH<sub>4</sub>/CO<sub>2</sub> flux ratio indicate that only about 0.01% of  
512 carbon mineralized is emitted as CH<sub>4</sub> (Figure 8).

513 Global air-sea CH<sub>4</sub> emissions upscaled from the total seagrass area of 160,387 – 266,562 km<sup>2</sup>  
514 were 13.0 ± 33.4 Tg CO<sub>2</sub>-eq yr<sup>-1</sup> (4.6 g C m<sup>-2</sup> yr<sup>-1</sup>) in 20-year time horizons, which would  
515 offset only 1.6% (maximum of 25%) of global seagrass carbon sequestration in soils (833 ±  
516 230 Tg CO<sub>2</sub> yr<sup>-1</sup> or 138 ± 38 g C m<sup>-2</sup> yr<sup>-1</sup>) (Table 5). Yet, both our measurements and the  
517 global estimates were mostly conducted across a short period of time. Therefore, long-term  
518 CH<sub>4</sub> flux measurements are required to cover the natural variability. Negligible CH<sub>4</sub> offset in  
519 both our site and global seagrass averages highlight that seagrasses are significant carbon  
520 sinks. Seagrass seems to emit less CH<sub>4</sub> than other coastal vegetated ecosystems such as  
521 mangroves and saltmarshes. For example, previous studies showed that methane emissions  
522 can offset <6% of carbon burial in a saltmarsh in China (Yau et al., 2022) and 18% in  
523 Australian mangroves receiving freshwater inputs (Rosentreter et al., 2018). Since seagrass  
524 are fully submerged and freshwater inputs are often limited, higher CH<sub>4</sub> oxidation in the  
525 water column could reduce CH<sub>4</sub> emissions relative to periodically inundated mangrove and  
526 saltmarsh systems. Overall, our study suggests that seagrass sequesters carbon without  
527 emitting large amounts of methane to the atmosphere.

528



529

530 **Figure 8.** Relationship between CO<sub>2</sub> flux and CH<sub>4</sub> flux in Station S across the study period.  
 531 The colour represents hour of the day. The solid line represents the fitted regression equation  
 532 ( $\pm$ SE), and the shaded area are the 95% confidence limits of the regression line, the  $r^2$  value  
 533 the degree of correlation, and the  $p$  value the level of significance.

534 **Table 4.** Global CH<sub>4</sub> air-sea and sediment-water emissions estimates from seagrass and the  
 535 carbon offset. The CH<sub>4</sub> flux for the seagrass is updated from (Rosentreter, Al-Haj, et al.,  
 536 2021).  $n$  refers to number of study sites.

Parameters			Air-sea	Sediment water
$n$			8	18
CH <sub>4</sub> flux	$\mu\text{mol CH}_4 \text{m}^{-2} \text{d}^{-1}$	Geomean <sup>a</sup>	30.1	26.1
	$\mu\text{mol CH}_4 \text{m}^{-2} \text{d}^{-1}$	Range	0.1 - 307.2	0.3 - 401.3
Area	$\text{km}^2$	Range	160,387 – 266,562 <sup>b</sup>	
Global CH <sub>4</sub> flux	$\text{Tg CH}_4 \text{yr}^{-1}$	Mean	0.03	0.02
	$\text{Tg CH}_4 \text{yr}^{-1}$	Range	0.00009 - 0.48	0.00028 - 0.62
SGWP <sub>100</sub>	$\text{Tg CO}_2\text{-eq yr}^{-1}$	Mean	1.3	1.1
SGWP <sub>20</sub>	$\text{Tg CO}_2\text{-eq yr}^{-1}$	Mean	2.7	2.3
Carbon burial*	$\text{g C m}^{-2} \text{yr}^{-1}$	Mean + SE		$138 \pm 38^c$
	$\text{g C m}^{-2} \text{yr}^{-1}$	Range		45 – 190
Global C burial	$\text{Tg C yr}^{-1}$	Mean + SE		$227 \pm 63$
Global C burial	$\text{Tg CO}_2 \text{yr}^{-1}$	Mean + SE		$833 \pm 230$
Offset of SGWP <sub>100</sub>	%	Mean	1.6	1.4
	%	Range	0.02 – 11.6	0.05 – 15.1
Offset of SGWP <sub>20</sub>	%	Mean	3.3	2.9
	%	Range	0.03 – 25	0.1 – 32

537

538 <sup>a</sup> Global geometric mean was calculated from the global compiled data set based on Table 3;  
539 <sup>b</sup> Global seagrass area from McKenzie et al., (2020); <sup>c</sup> Global carbon burial was extracted  
540 from Mcleod et al., (2011).

## 541 **5 Conclusion**

542 Our continuous timeseries observations provide new insights into the spatial and diel patterns  
543 of CH<sub>4</sub> sediment-water and air-sea fluxes in seagrass-dominated ecosystems. Small CH<sub>4</sub>  
544 emissions to the atmosphere were measured in the coastal bay dominated by *P.oceanica*.  
545 Porewater profiles reflected methanogenesis activity in deep sediments. The link between  
546 <sup>222</sup>Rn concentrations and the higher sediment-water to air-sea CH<sub>4</sub> fluxes suggested that  
547 sediments were the main source of CH<sub>4</sub> emissions to the atmosphere. CH<sub>4</sub> oxidation in the  
548 water column, supported by photosynthesis in seagrass, seem to explain the low CH<sub>4</sub>  
549 emissions in the dense seagrass areas. The high spatial variability of CH<sub>4</sub> within the bay  
550 highlights the importance of seagrass in regulating CH<sub>4</sub> emissions and/or the dilution by  
551 oceanic water. More continuous, high resolution CH<sub>4</sub> measurements are required to resolve  
552 the potential diel patterns and the role of seagrass in CH<sub>4</sub> emissions.

553 Our study highlights the importance of differentiating air-sea and sediment-water flux when  
554 estimating seagrass CH<sub>4</sub> emissions. A low CH<sub>4</sub> offset to carbon burial was estimated both on  
555 local and global scale seagrass meadows. More site-specific carbon burial and long-term  
556 emission estimates are needed to resolve CH<sub>4</sub> dynamics in seagrass carbon budgets. The  
557 current evidence suggests minor offsetting of carbon sequestration by seagrass CH<sub>4</sub>  
558 emissions.

559

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