

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

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Abstract

Seagrass meadows are effective carbon sinks due to their high primary production and sequestration in sediments. However, methane (CH₄) fluxes can partially counteract their carbon sink capacity. Here, we measured diffusive sediment-water and air-sea CO₂ and CH₄ fluxes in a coastal embayment dominated by *Posidonia oceanica* in the Mediterranean Sea. High resolution timeseries observations revealed large spatial and temporal variability in CH₄ concentrations (2 to 36 nM). Higher emissions were observed in an area with dense seagrass meadows. A 6 - 40% decrease of CH₄ concentration in the surface water around noon indicates that photosynthesis likely limits CH₄ fluxes. Sediments were the major CH₄ source as implied from radon (a natural porewater tracer) observations and evidence for methanogenesis in deeper sediments. CH₄ 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 CH₄ emissions ($0.12 \pm 0.10 \mu\text{mol m}^{-2} \text{d}^{-1}$), suggesting that dilution and CH₄ oxidation in the water column could reduce net CH₄ fluxes into the atmosphere. Overall, relatively low air-sea CH₄ fluxes at this likely represent net emissions from subtidal seagrass habitats sites, which are not influenced by nearby allochthonous CH₄ sources. The local CH₄ 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 CH₄ 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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21 **Key Points:**

- 22 • High resolution CH₄ observations reveal diel cycles linked to seagrass productivity
- 23 • Sediments were the main CH₄ source in both living and dead seagrass areas
- 24 • CH₄ 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 (CH₄) fluxes can partially counteract their
39 carbon sink capacity. Here, we measured diffusive sediment-water and air-sea CO₂ and CH₄
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 CH₄
42 concentrations (2 to 36 nM). Higher emissions were observed in an area with dense seagrass
43 meadows. A 6 – 40% decrease of CH₄ concentration in the surface water around noon
44 indicates that photosynthesis likely limits CH₄ fluxes. Sediments were the major CH₄ source
45 as implied from radon (a natural porewater tracer) observations and evidence for
46 methanogenesis in deeper sediments. CH₄ 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 CH₄ emissions ($0.12 \pm 0.10 \mu\text{mol m}^{-2} \text{d}^{-1}$),
48 suggesting that dilution and CH₄ oxidation in the water column could reduce net CH₄ fluxes
49 into the atmosphere. Overall, relatively low air-sea CH₄ fluxes at this likely represent net
50 emissions from subtidal seagrass habitats sites, which are not influenced by nearby
51 allochthonous CH₄ sources. The local CH₄ 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 CH₄ 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 (CH₄).
59 Methane has a 45 – 96 times more powerful global warming effect than carbon dioxide. If
60 seagrass meadows release CH₄, the emissions counteract their climate mitigation potential.
61 We measured greenhouse gas concentrations and fluxes in a seagrass-dominated
62 Mediterranean embayment. Low CH₄ coincided with the increase of oxygen produced
63 through seagrass photosynthesis. Areas with dense seagrass meadows had lower CH₄
64 emissions. Overall, the seagrass-dominated bay was a small source of CH₄ 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 (CO₂) 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⁻¹) 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 CO₂ 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 CO₂ and CH₄ to the atmosphere
93 (Carnell et al., 2020; Lyimo et al., 2018).

94

95 The coastal ocean is a hotspot of CH₄ emissions, contributing with 75% of the global oceanic
96 CH₄ emissions (Weber et al., 2019). While seagrass meadows store organic carbon, the high
97 sediment organic matter content also favors methane (CH₄) production (Rosentreter, Al-Haj,
98 et al., 2021). CH₄ 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 CH₄ emissions (Egger, Kraal, et al., 2016). The presence of methylated compounds in
103 seagrass rhizosphere provide another pathway for CH₄ production, even in dead seagrass
104 meadows (Schorn et al., 2022). The net CH₄ 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 CH₄ fluxes to the atmosphere.

108 Since CH₄ is a potent greenhouse gas with 45–96 times greater sustained-flux warming
109 potential (SGWP) than CO₂ (Neubauer & Megonigal, 2015), the efficiency of seagrasses as a
110 carbon sink can be partially offset by CH₄ emissions. Although measurements of CH₄ 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), CH₄ fluxes in seagrass meadows
113 remain poorly constrained across multiple spatial and temporal scales. The air-sea and
114 sediment-water CH₄ fluxes from seagrass ranged from 0 to 400 μmol m⁻² d⁻¹, resulting in
115 global upscaled fluxes of 0.18 Tg CH₄ per year (Al-Haj et al., 2022). Several seagrass
116 meadow CH₄ 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 CH₄ propagates through the shallow water column and reaches the
119 atmosphere unmodified.

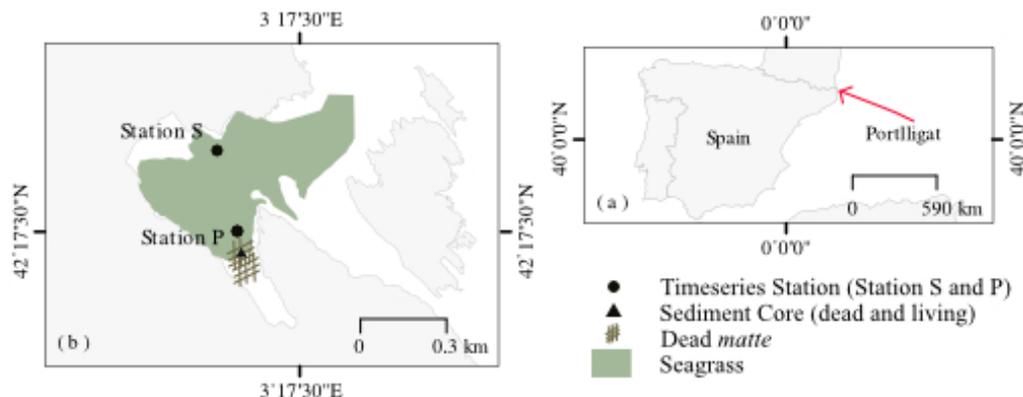
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121 Here, we report high resolution timeseries observations of dissolved CH₄ over multiple diel
122 cycles and estimate sediment-water and air-sea CH₄ fluxes in *P. oceanica* meadows at a
123 Mediterranean bay. We quantified air-sea CO₂ and CH₄ fluxes above the seagrass using
124 automated, *in situ* surface water observations (including ²²²Rn measurements, a natural
125 porewater tracer), and at the sediment-water interface using sediment cores. This study aims
126 to (1) estimate sediment-water CH₄ fluxes, (2) evaluate the spatial and diel variability of air-
127 sea CH₄ fluxes, (3) assess the fate of CH₄ by comparing CH₄ sediment-water fluxes and air-
128 sea fluxes, and (4) examine whether CH₄ 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 km²). 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⁻²) 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 11th to 18th 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 16th
 157 September with a maximum 2.9 cm hr⁻¹.

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 ²²²Rn-air
 161 analyzer (RAD7), while CO₂ and CH₄ 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⁻¹ to the showerhead
 165 gas exchange. There were data gaps in the patchy seagrass due to instrument failure (days
 166 13th and 14th September 2021). CO₂ and CH₄ 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 ²²²Rn, CO₂ and CH₄ 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 ²²²Rn, CO₂ and CH₄ across the bay covering a
 171 track of 1.5 km on 18th September 2021 from 16:00 to 17:30 using the same experimental
 172 setup as described above. CH₄ fluxes for the whole bay area were found using inverse
 173 distance weighted interpolation methods, from which an average was obtained.. Solubility of
 174 CO₂ and CH₄ 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 CH₄ 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 N₂ flushed vial using a gas-tight syringe. The headspace CH₄
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 [CH₄] is the porewater CH₄ 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⁻¹ mol⁻¹), *T* is the laboratory
198 temperature (°C) and *ϕ* 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 CH₄ and CO₂ flux**

213 The sediment-water CO₂ and CH₄ 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 CH₄ and DIC (μmol m⁻² d⁻¹), *ϕ* is the sediment porosity, *D_S* is the
216 sediment diffusion coefficient (cm² s⁻¹), *C* is the CH₄ 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 CH₄ and DIC seawater at 20°C was 1.39×10^{-9} and 9.89×10^{-10} (Lerman,
 221 1979). Tortuosity (θ) was calculated from sediment porosity using $\theta = 1 - \ln(\phi^2)$
 222 (Boudreau, 1997; Lengier et al., 2021).

223

224 The air-sea CO₂ and CH₄ 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 CO₂ and CH₄ flux ($\text{mmol m}^{-2} \text{d}^{-1}$), k represents gas transfer velocity (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 (μatm) of
 229 CO₂ and CH₄ in water and air, respectively. The atmospheric partial pressures of CO₂ and
 230 CH₄ 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 (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 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 (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, CH₄ flux was converted to CO₂ equivalents. CH₄
 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 CO₂ equivalent emissions of CH₄ 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 CH₄ flux ($\mu\text{mol m}^{-2} \text{d}^{-1}$); A is the area of seagrass (km^2),
 248 SGWP of 100 and 20 years of 45 and 96, f is the conversion factor from μmol to Tg

249 To investigate whether CO₂ and CH₄ 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**

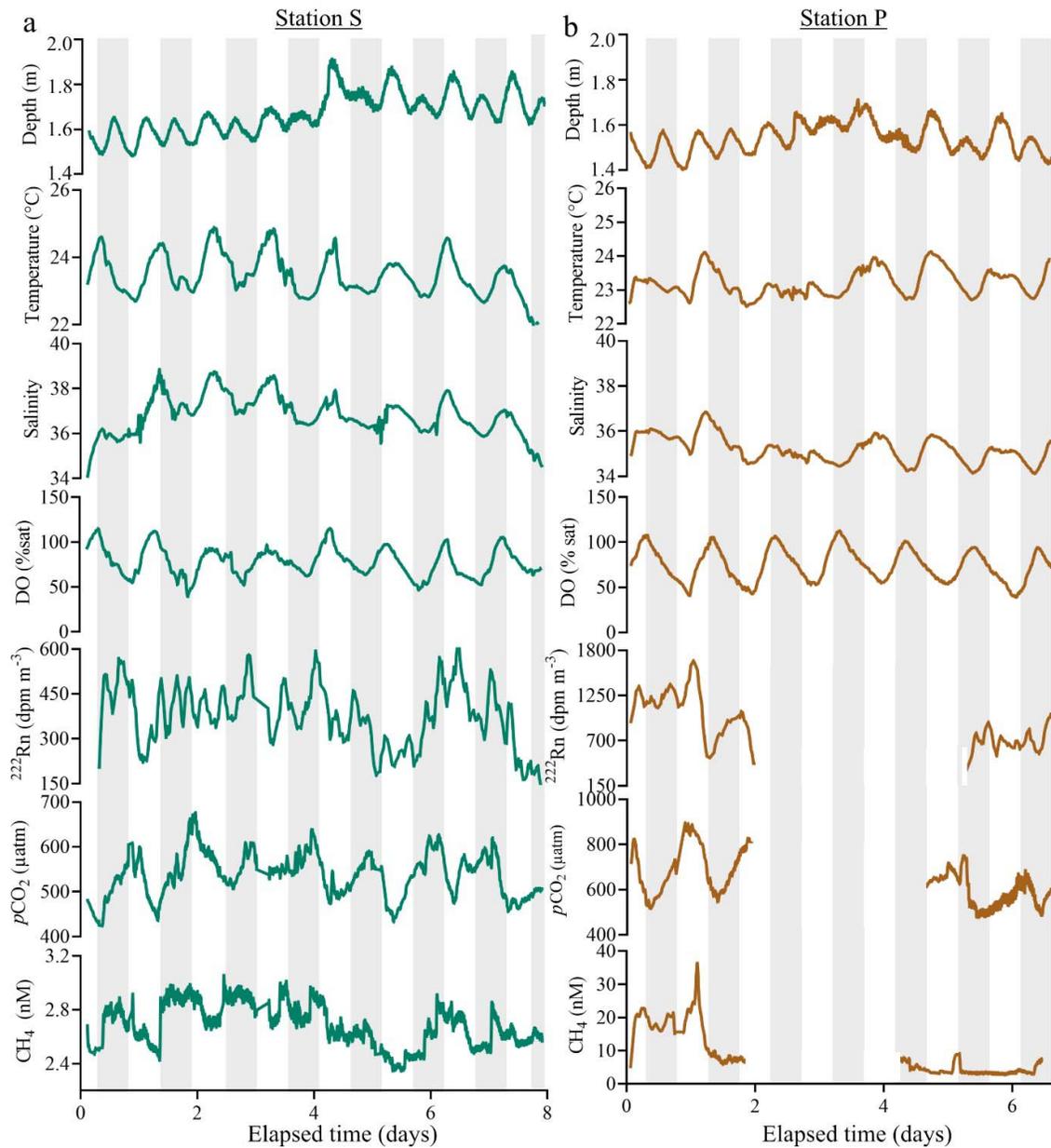
256 The average water temperature and salinity were similar at Stations S and P, with 23.3 ± 0.7
257 °C (SD) and 36 ± 1 respectively (Figure 2). The water depth ranged from 1.4 to 2.4 m and
258 wind speeds at 10 m above sea level averaged $2.1 \pm 1.6 \text{ m s}^{-1}$ over the study period. The light
259 intensity under the water was higher in Station P ($1747 \pm 633 \text{ lum ft}^{-2}$) than Station S ($1044 \pm$
260 670 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 CH₄
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 CH₄ 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 CH₄ and CO₂ 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 CH₄ at both
270 sites and both stations exhibited a weak but significant correlation between DO saturation and
271 CH₄ (Figure 7). The hourly average CH₄ concentration had a hysteretic pattern to light
272 intensity in Station S but a strong correlation in Station P. However, ²²²Rn did not follow a
273 diel pattern at both stations.

274 **3.2 Spatial variation**

275 $p\text{CO}_2$ and CH₄ 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 CH₄ concentrations were five times lower in
279 Station S ($2.68 \pm 0.17 \text{ nM}$) compared to Station P ($8.57 \pm 6.72 \text{ nM}$). ²²²Rn 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 m^{-3}) (Figure 2). The high CH₄ concentrations at Station P (peak at 36.3 nM at 13:00) occurred
282 in the first two days of observations coinciding with the high concentrations of ²²²Rn (peak at
283 1886 dpm m^{-3}) and high irradiance (6000 lum ft^{-2}) (Figure 3). ²²²Rn concentrations were
284 positively correlated with CH₄ 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 CH₄ emissions were observed in both stations,
286 with one order of magnitude higher CH₄ 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 CO₂ 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 CH₄ and CO₂ emissions were calculated from four different gas transfer models. CH₄
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.



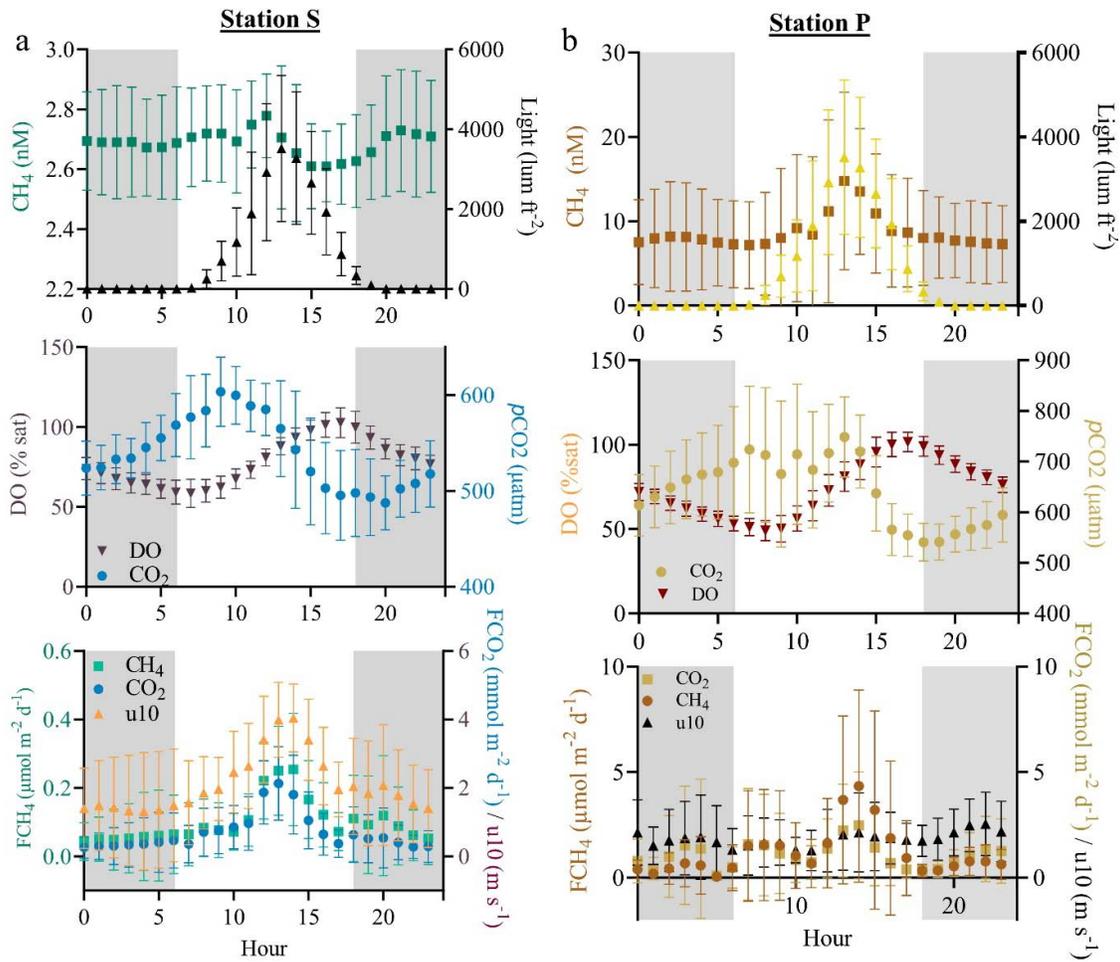
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295 **Figure 2.** Timeseries observations of dissolved greenhouse gases and ancillary parameters at
296 (a) Station S; and (b) Station P. The shaded area indicates nighttime, whereas the non-shaded
297 area indicates daytime. Gaps in the data were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

298

299

300



301

302 **Figure 3.** Mean ± standard deviation of hourly concentration of CH₄ (nM), CO₂ (*p*CO₂), light
 303 light intensity (lum ft⁻²), percentage saturation of dissolved oxygen (DO, % sat), wind speed at 10
 304 m above sea level (u10), CO₂ fluxes (FCO₂), and CH₄ fluxes (FCH₄) at Station S (left) and
 305 Station P (right) over the period of study. Both CO₂ and CH₄ 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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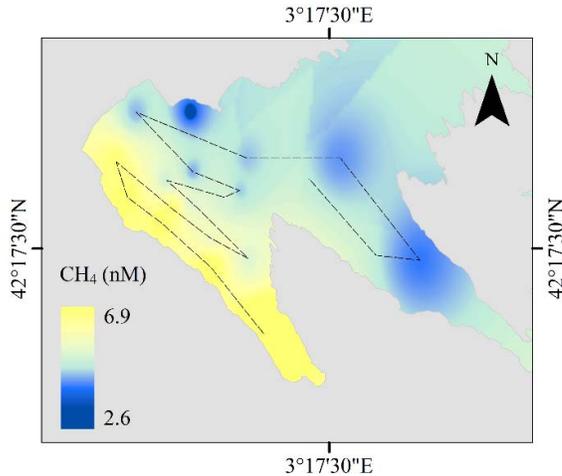
317 **Table 2.** A summary of environmental parameters and GHG fluxes measured simultaneously
 318 at Station S and Station P. Day indicates data from 06:00 to 18:00 and night indicates data
 319 from 18:00 to 06:00. All data are reported as mean \pm SD. The air-sea CO₂ and CH₄ fluxes
 320 were calculated 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).

	Unit	Station S			Station P			Spatial Survey
		Overall	Day	Night	Overall	Day	Night	Overall
Description		<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 ⁻¹	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 ⁻²	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 ⁻¹	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 ₂	μatm	538 \pm 50	561 \pm 41	522 \pm 27	632 \pm 103	677 \pm 36	614 \pm 20	606 \pm 51
CH ₄	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
²²² Rn	dpm m ⁻³	377 \pm 129	392 \pm 159	376 \pm 130	892 \pm 331	863 \pm 128	933 \pm 81	/
CO₂ flux								
R&C	mmol m ⁻² d ⁻¹	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 ⁻² d ⁻¹	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 ⁻² d ⁻¹	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 ⁻² d ⁻¹	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
CH₄ flux								
R&C	μmol m ⁻² d ⁻¹	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 ⁻² d ⁻¹	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 ⁻² d ⁻¹	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 ⁻² d ⁻¹	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⁻¹)
 326 lower than the average timeseries measurements (2.2 m s⁻¹). CH₄ concentrations varied across
 327 the bay, ranging from 2.6 to 6.9 nM. The highest CH₄ 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 CH₄ was estimated for the whole bay, ranging from
 331 0.12 \pm 0.10 to 2.97 \pm 1.47 μmol m⁻² d⁻¹, depending on the gas transfer model used. The
 332 spatial survey represents the average of whole bay (0.21 km²), 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 CH₄ emissions, we used the average CH₄ flux for the whole bay to account
 335 for the spatial differences.

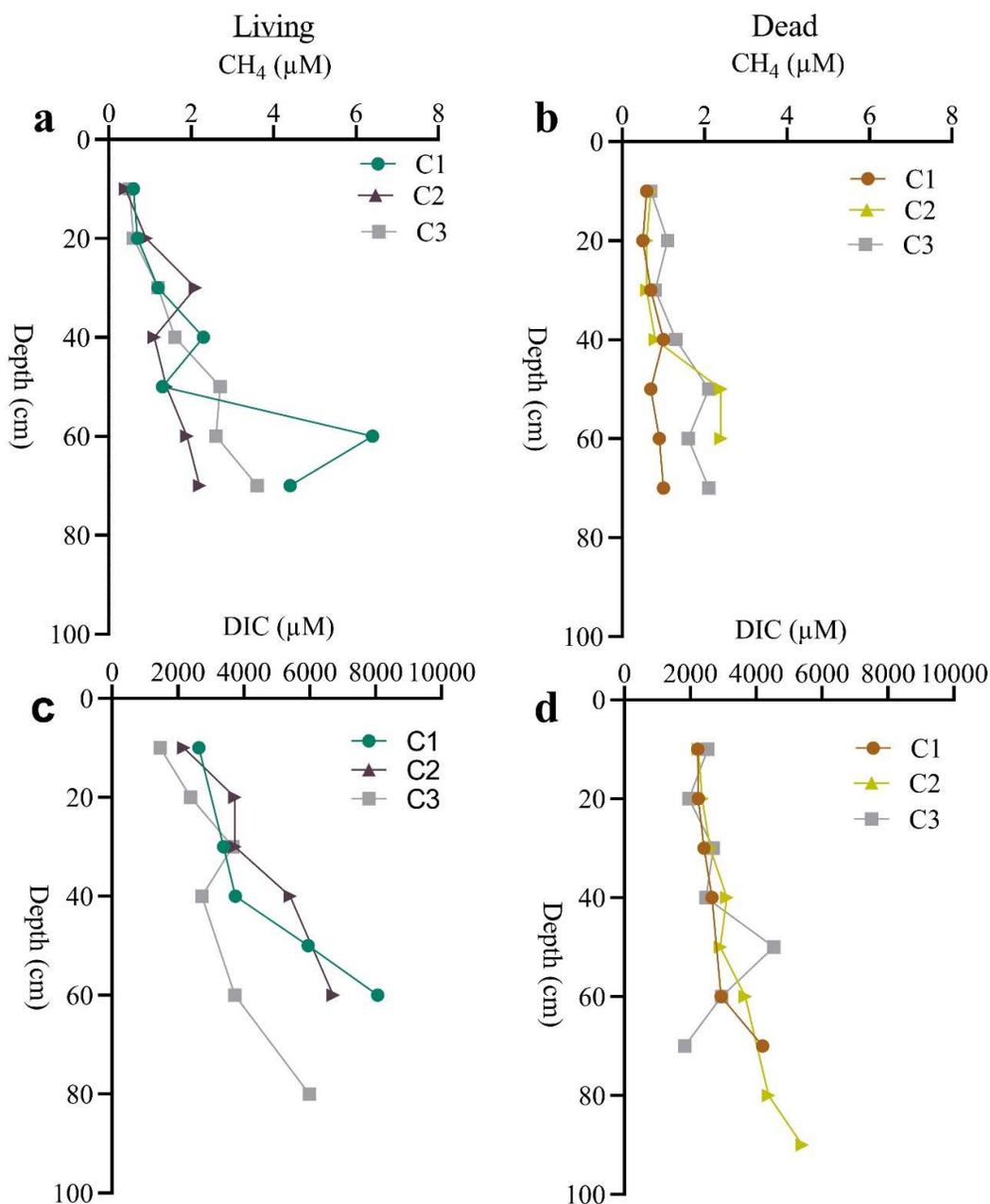


336

337 **Figure 4.** The distribution of CH₄ 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 CH₄ concentration in living seagrass cores were two-times higher than in the dead
 344 seagrass. Both cores showed similar CH₄ depth profiles, increasing from 1 μM at the surface
 345 up to 6 μM at 50 cm (Figure 5). The estimated sediment diffusive CH₄ flux in living seagrass
 346 (0.1 – 0.4 μmol m⁻² d⁻¹) was 2 to 11 times higher than in dead seagrass (0 – 0.1 μmol m⁻² d⁻¹).
 347 CH₄ sediment-water fluxes in the living seagrass were 2.5 times higher than CH₄ air-sea
 348 emissions in the Station S (i.e., seagrass-dominated site), whereas sediment-water CH₄ 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⁻² d⁻¹) was three-times higher than in the dead seagrass
 356 (68 – 88 μmol m⁻² d⁻¹).



357

358 **Figure 5.** Vertical sediment profiles of porewater CH₄ 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 CH₄ 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 ^a	g cm ⁻³	0.2 ± 0.1	0.3 ± 0.1
Water content ^a	%	51 ± 5.1	46 ± 4.9
Particulate Organic matter ^a	%	16.9 ± 7.4	17.5 ± 7.4

DIC	μM	4094 \pm 1827	2974 \pm 939
CH ₄	μM	2.3 \pm 1.5	1.1 \pm 0.6
CH ₄ 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 ^aAverage of the first 50 cm of the sediment

364

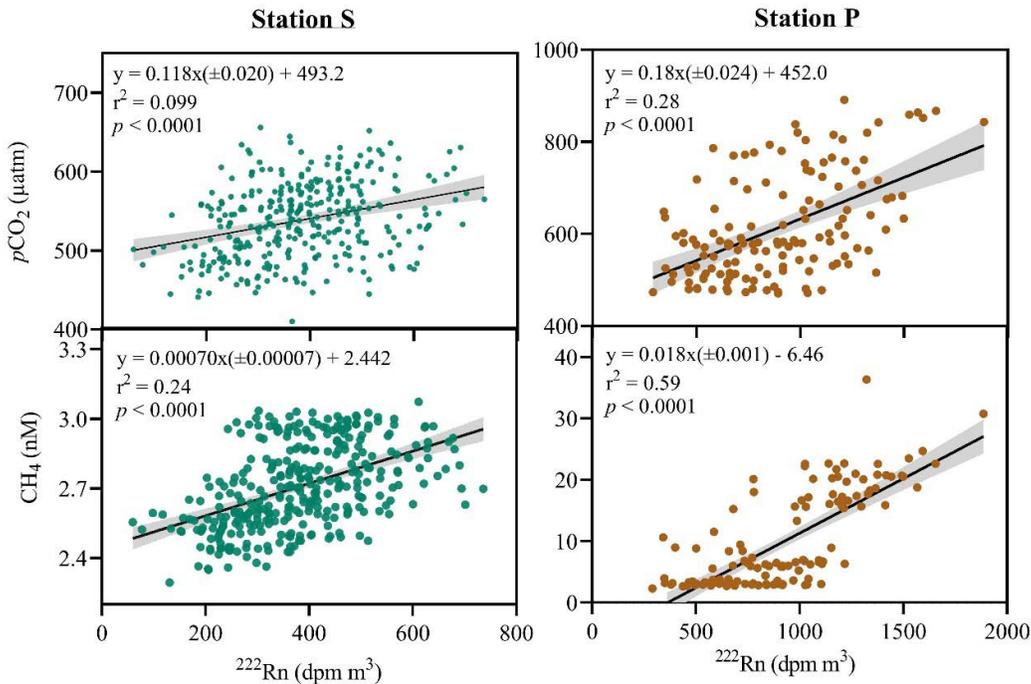
365 4 Discussion

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 CH₄ effluxes. The high porewater CH₄
 369 concentration (0.3 – 2.1 μM) 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 μM), but similar
 371 to those estimated for *Zostera noltii* in France (2.5 – 8 μM) (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 CH₄ production below 40 – 50 cm sediments in seagrass sediments compared to the relative
 375 flat CH₄ 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 CH₄ consumption could occur
 377 in upper layer (Schorn et al., 2022). Positive correlations between the porewater tracer ²²²Rn
 378 and CH₄ concentrations also suggested that the sediments underlying the seagrasses are the
 379 main source of CH₄ (and ²²²Rn) into the environment (Figure 6). There are no other major
 380 ²²²Rn 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 CH₄ production. A positive relationship between
 384 porewater DIC and CH₄ concentrations suggested that methanogenesis supports organic
 385 carbon mineralization (Aleksandra & Katarzyna, 2018). Both DIC and CH₄ 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 O₂ 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 CH₄
 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 CH₄: DIC, the contribution of methanogenesis to total carbon
 393 mineralization was at maximum 0.03%.

394 Our CH₄ 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 CH₄ due to the production of methylated compounds that fuels
 400 methanogenesis (Schorn et al. 2022).



401

402 **Figure 6.** Scatter plot of ^{222}Rn against 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.

406

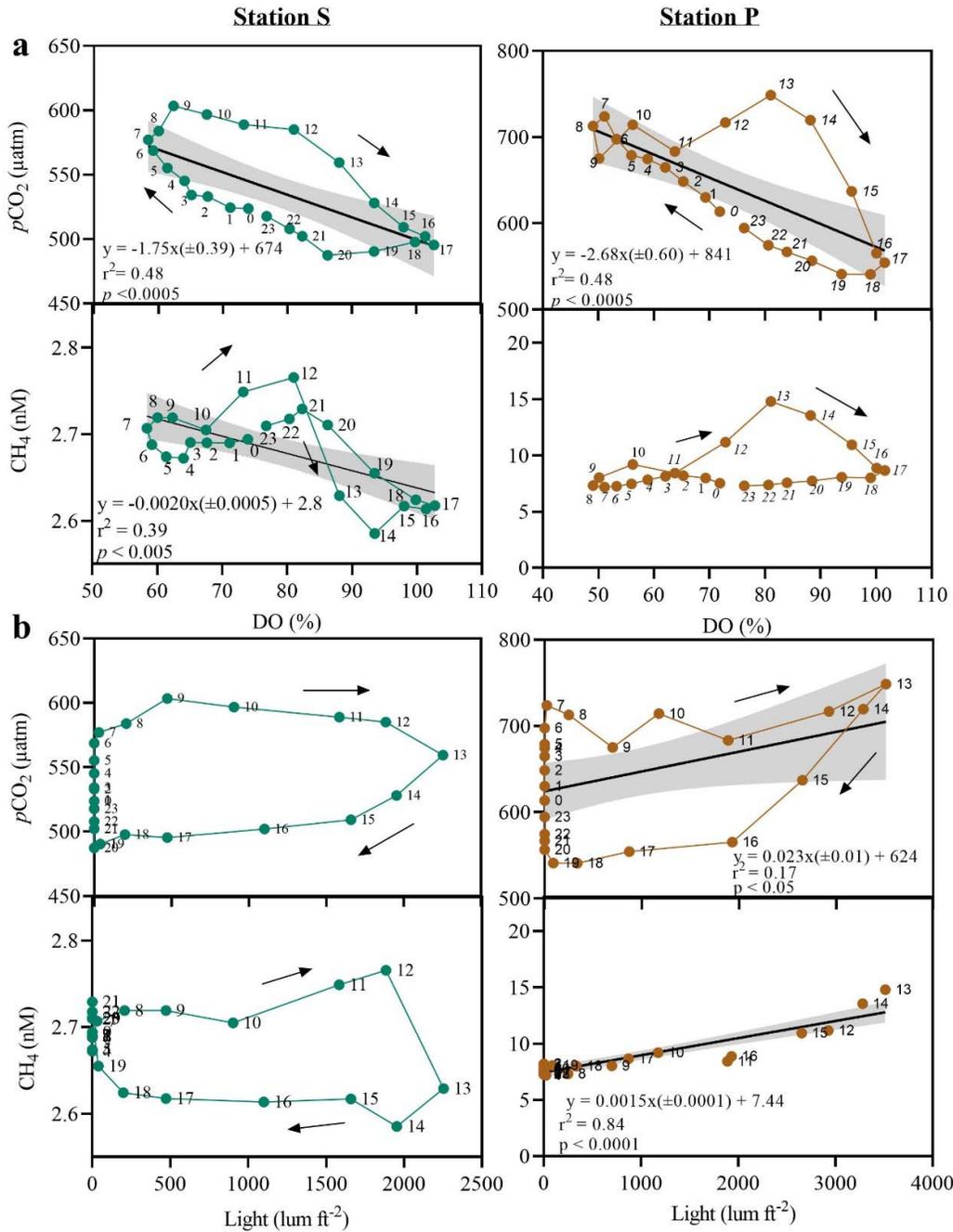
407 4.2 Diel pattern in air-sea fluxes of CH_4

408 A diel air-sea CH_4 pattern with a decreasing trend in afternoon suggests that oxygen
 409 availability can control CH_4 emissions to the atmosphere (Figure 3). A 6% to 40% decrease
 410 of CH_4 concentrations in the afternoon coinciding with increasing DO and high light intensity
 411 indicates higher 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 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 CH_4 emissions in a tropical seagrass
 416 meadow. Lower air-sea CH_4 emissions in the dense seagrass site (Station S) further
 417 demonstrates that photosynthesis could limit CH_4 emissions. The diel CH_4 variation likely
 418 implied that the productivity of seagrass drives the oxidation rate of CH_4 , controlling CH_4
 419 emissions.

420 The patchy seagrass contributed to a higher CH_4 flux than the dense seagrass and exhibited a
 421 more pronounced CH_4 peak during noon, which was not observed in the dense seagrass. This
 422 CH_4 peak could be produced during photosynthesis of submerged photosynthetic organisms
 423 as ebullition or through direct CH_4 production, including seagrass, cyanobacteria and algae
 424 during (Hilt et al., 2022). The positive correlation of light intensity with CH_4 concentrations
 425 observed only in patchy seagrass might suggest abiotic CH_4 photoproduction (Figure 7). A

426 peak of CH₄ 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 CH₄ production
430 (Schorn et al., 2022). More studies are needed to understand the contribution of both seagrass
431 meadows and dead matte habitat to CH₄ production.

432 The high spatial differences in CH₄ concentrations could link to the proximity to the open
433 ocean. The patchy seagrass area had two-times higher ²²²Rn concentrations and ten-times
434 greater CH₄ fluxes than the area with dense seagrass. As the dense seagrass site was closer to
435 the open ocean, ocean waters could dilute CH₄ concentration within the area, resulting in a
436 lower CH₄ and ²²²Rn 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 CH_4 and 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 CH₄ emissions on local and global scales**

448 The average air-sea CH₄ 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 CH₄ 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 CH₄ emissions.

456 Another reason for our relatively low CH₄ flux could be the lack of other freshwater sources
457 at our study site. Methane-enriched freshwater inputs could result in overestimates of CH₄
458 fluxes within seagrass meadows. The air-water CH₄ 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 CH₄ 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 CH₄ concentration in porewater drives the high surface water CH₄
468 (Call et al., 2018; Santos et al., 2019; Yau et al., 2022). Flanking saltmarshes adjacent to
469 seagrass export CH₄, elevating CH₄ 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 CH₄ air-sea fluxes likely represent emissions from subtidal seagrass
472 habitats.

473 We combined our results with the literature to re-evaluate global CH₄ 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 CH₄
476 from the sediment to water but do not account for the exchange of CH₄ across the water-air
477 interface or potentially CH₄ 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 CH₄ fluxes. Earlier global estimates of seagrass CH₄ 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 CH₄ (20 sites) fluxes in seagrass meadows (Table 4). Both air-sea and sediment-water
485 CH₄ fluxes are highly variable. The geometric mean of air-sea and sediment-water CH₄
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 ± 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 CH₄ 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 (CH₄) 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 CH₄ fluxes represent the global average.

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

494

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

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

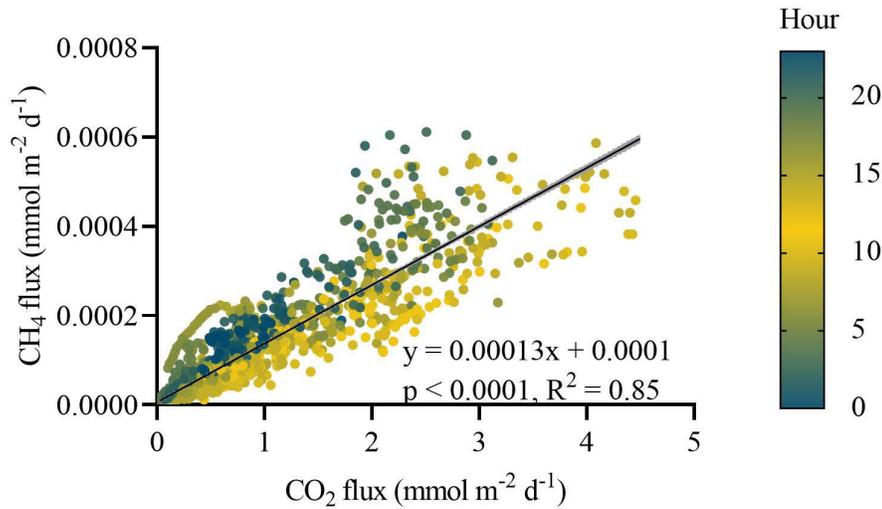
499 [Asplund et al., 2022](#)

500 **4.4 Implications for net carbon sequestration**

501 To evaluate the global warming potential of CH₄ emissions in seagrass and the potential
502 offset from carbon burial benefits, air-sea CH₄ fluxes were converted to CO₂-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 CH₄ fluxes
506 in Portilligat bay are equivalent to 0.05 and 0.03 g CO₂-eq m² yr⁻¹ 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⁻² yr⁻¹ (Serrano et al., 2016). Therefore, the estimated air-sea
509 CH₄ emissions from *P. oceanica* in our site offset the carbon burial only by < 0.7 % in a 20-
510 year time horizon. The low CH₄ offset is attributed to the low CH₄ flux and high carbon
511 burial of *P. oceanica*. Our average CH₄/CO₂ flux ratio indicate that only about 0.01% of
512 carbon mineralized is emitted as CH₄ (Figure 8).

513 Global air-sea CH₄ emissions upscaled from the total seagrass area of 160,387 – 266,562 km²
514 were 13.0 ± 33.4 Tg CO₂-eq yr⁻¹ (4.6 g C m⁻² yr⁻¹) 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 CO₂ yr⁻¹ or 138 ± 38 g C m⁻² yr⁻¹) (Table 5). Yet, both our measurements and the
517 global estimates were mostly conducted across a short period of time. Therefore, long-term
518 CH₄ flux measurements are required to cover the natural variability. Negligible CH₄ offset in
519 both our site and global seagrass averages highlight that seagrasses are significant carbon
520 sinks. Seagrass seems to emit less CH₄ 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 CH₄ oxidation in the
525 water column could reduce CH₄ 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 CO₂ flux and CH₄ 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 CH₄ air-sea and sediment-water emissions estimates from seagrass and the
 535 carbon offset. The CH₄ 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 ₄ flux	$\mu\text{mol CH}_4\text{m}^{-2}\text{d}^{-1}$	Geomean ^a	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	km^2	Range	160,387 – 266,562 ^b	
Global CH ₄ 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 ₁₀₀	$\text{Tg CO}_2\text{-eq yr}^{-1}$	Mean	1.3	1.1
SGWP ₂₀	$\text{Tg CO}_2\text{-eq yr}^{-1}$	Mean	2.7	2.3
Carbon burial*	$\text{g C m}^{-2}\text{yr}^{-1}$	Mean + SE		138 ± 38^c
	$\text{g C m}^{-2}\text{yr}^{-1}$	Range		45 – 190
Global C burial	Tg C yr^{-1}	Mean + SE		227 ± 63
Global C burial	$\text{Tg CO}_2\text{ yr}^{-1}$	Mean + SE		833 ± 230
Offset of SGWP ₁₀₀	%	Mean	1.6	1.4
	%	Range	0.02 – 11.6	0.05 – 15.1
Offset of SGWP ₂₀	%	Mean	3.3	2.9
	%	Range	0.03 – 25	0.1 – 32

537

538 ^a Global geometric mean was calculated from the global compiled data set based on Table 3;
539 ^b Global seagrass area from McKenzie et al., (2020); ^c 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 CH₄ sediment-water and air-sea fluxes in seagrass-dominated ecosystems. Small CH₄
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 ²²²Rn concentrations and the higher sediment-water to air-sea CH₄ fluxes suggested that
547 sediments were the main source of CH₄ emissions to the atmosphere. CH₄ oxidation in the
548 water column, supported by photosynthesis in seagrass, seem to explain the low CH₄
549 emissions in the dense seagrass areas. The high spatial variability of CH₄ within the bay
550 highlights the importance of seagrass in regulating CH₄ emissions and/or the dilution by
551 oceanic water. More continuous, high resolution CH₄ measurements are required to resolve
552 the potential diel patterns and the role of seagrass in CH₄ emissions.

553 Our study highlights the importance of differentiating air-sea and sediment-water flux when
554 estimating seagrass CH₄ emissions. A low CH₄ 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 CH₄ dynamics in seagrass carbon budgets. The
557 current evidence suggests minor offsetting of carbon sequestration by seagrass CH₄
558 emissions.

559

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