



Assessing methane emissions and soil carbon stocks in the Camargue coastal wetlands: Management implications for climate change regulation

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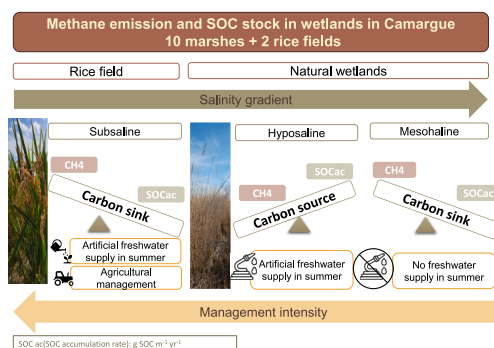
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HIGHLIGHTS

- Carbon budget over a salinity and management gradient in wetlands was assessed.
- Low-salinity wetlands in Camargue are crucial for carbon budget.
- CH₄ in low-salinity wetlands with artificial freshwater supply offset SOC storage.
- Rice fields emit less CH₄ than marshes and present high SOC storage.
- The altered hydrology for leisure activities in the marshes needs to be reevaluated.

GRAPHICAL ABSTRACT



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ABSTRACT

Coastal wetlands are crucial in climate change regulation due to their capacity to act as either sinks or sources of carbon, resulting from the balance between greenhouse gas (GHG) emissions, mainly methane (CH₄), and soil carbon sequestration. Despite the paramount role of wetlands in climate regulation few studies investigate both aspects. The Camargue is one of the largest wetlands in Europe, yet the ways in which environmental and anthropic factors drive carbon dynamics remain poorly studied. We examined GHG emissions and soil organic carbon (SOC) stocks and accumulation rates in twelve representative wetlands, including two rice fields, to gain insights into the carbon dynamics and how it is influenced by hydrology and salinity. Mean CH₄ rates ranged between -87.0 and $131.0 \text{ mg m}^{-2} \text{ h}^{-1}$ and the main drivers were water conductivity and redox, water table depth and soil temperature. High emission rates were restricted to freshwater conditions during summer flooding

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periods whereas they were low in wetlands subjected to summer drought and water conductivity higher than 10 mS cm^{-1} . Nitrous oxide emissions were low, ranging from -0.5 to $0.9 \text{ mg N}_2\text{O m}^{-2} \text{ h}^{-1}$. The SOC stocks in the upper meter ranged from 17 to 90 Mg OC ha^{-1} . Our research highlights the critical role of low-saline wetlands in carbon budgeting which potentially are large sources of CH_4 but also contain the largest SOC stocks in the Camargue. Natural hydroperiods, involving summer drought, can maintain them as carbon sinks, but altered hydrology can transform them into sources. Artificial freshwater supply during summer leads to substantial CH_4 emissions, offsetting their SOC accumulation rates. In conclusion, we advocate for readjusting the altered hydrology in marshes and for the search of management compromises to ensure the compatibility of economic and leisure activities with the preservation of the inherent climate-regulating capacity of coastal wetlands.

1. Introduction

Coastal wetlands, such as mangroves and saltmarshes, play a pivotal role in the regulation of climate change, primarily due to their exceptional efficiency in carbon sequestration—referred to as blue carbon (Chmura et al., 2003; McLeod et al., 2011). Their carbon burial rates per unit area surpass those of other terrestrial ecosystems (McLeod et al., 2011), rendering them crucial elements for climate change mitigation. However, wetlands globally contribute approximately 20–30 % of emissions in terms of Global Warming Potential (Bousquet et al., 2006; Saunio et al., 2016; Yuan et al., 2022). They are a primary natural source of methane (CH_4) emissions, a potent greenhouse gas (GHG) with a warming potential 28 times greater than that of CO_2 over a 100-year period (Myhre et al., 2013). In addition, they can also potentially emit nitrous oxide (N_2O) under soil aerobic conditions, which can occur for instance after severe dry periods, which are projected to be more frequent in the Mediterranean (Zittis et al., 2021). This GHG has a large warming potential, 265 times greater than CO_2 (Myhre et al., 2013), and thus even low emissions during short periods can impact on the warming effect of the wetlands. Consequently, the ability of coastal wetlands to mitigate climate change through carbon sequestration may be, at least partially, offset by GHG emissions (Holm et al., 2016). Despite the paramount role of wetlands in climate regulation, numerous studies have only separately evaluated GHG emissions (Holm et al., 2016; Keshta et al., 2023) and carbon sequestration (Choi and Wang, 2004; Fennessy et al., 2019), with fewer (e.g., Arias-Ortiz et al., 2021) investigating both aspects within the same study.

The hydrology and conductivity regimes of wetlands, alongside temperature, constitute the principal natural drivers of carbon dynamics (Bartlett and Harriss, 1993; Ardón et al., 2018). In addition, human factors also affect the capacity of wetlands to mitigate climate change, with the potential to transition wetlands from net carbon sinks to sources of carbon. These anthropogenic effects may arise from climate change effects such as increasing temperatures, sea level rise, or shifting precipitation patterns (Belenguer-Manzanedo et al., 2021), as well as from direct human action, including land-use changes (Looman et al., 2019), e.g., agriculture, or alterations in natural hydroperiods.

Deltas are highly productive systems that have historically supported a significant portion of global human population (approximately 4.5 % in 2017), despite covering just 0.57 % of the Earth's land surface area (Edmonds et al., 2020). This human presence has led to extensive alterations within these ecosystems, compromising their ability to provide vital ecosystem services such as water purification, soil fertility, biodiversity conservation, food production, and climate regulation. With a surface area of 1600 km^2 , the Camargue is one of the largest deltas of the Mediterranean Sea, second after the Nile delta, located in the mouth of the Rhône River (southern France) (Grillas, 2018). It is a micro-tidal socio-ecosystem (Boudouresque et al., 2020) where hydroperiods are mainly influenced by climatic conditions and human regulation. The delta comprises a wide variety of habitats, wherein 60 % of the area is covered by different types of wetlands (temporary marshes and ponds, salt steppes, salt pans) and 35 % by agricultural land, including rice fields. This diversity of habitats reflects a diverse range of hydrological regimes and salinities linked to its formation but also to management,

which modifies the natural gradients through dyking and massive imports of freshwater (about $4 \times 10^{11} \text{ m}^3 \text{ year}^{-1}$ for agricultural production, hunting activities, and management of marshes for nature conservation purposes) and of seawater (saltworks). Since the mid-20th century, water management in the Camargue has undergone substantial changes, notably marked by the expansion of rice cultivation and intensified wetland management, leading to an increase in the duration of freshwater flooding and a subsequent reduction in salinity in many of the system's marshes (Aguesse and Marazanof, 1965; Molinier and Tallon, 1974; Tamisier and Grillas, 1994; Dehorter and Tamisier, 1996). Simultaneously, human-driven effects in the opposite direction have also occurred: intensified management for salt production has expanded the surface area of the salt marshes with a reversal of the hydrological cycle and an increase in salinity (Britton and Johnson, 1987; Sadoul et al., 1996).

The objective of this study was to assess the GHG emissions, and the soil carbon stocks and accumulation rates along salinity and hydrology gradients in the Camargue wetlands. The results were examined to assess the effect of human-altered hydrology and salinity on the carbon budgets over a range of intensity management degrees.

2. Materials and methods

Twelve wetlands, including two rice fields cultivated according to the standard agricultural practices in France, were studied. The selection of these study sites ensured representation of the main types of wetland habitats (87 % of the wetland habitats in the Camargue delta according to a land use analysis of the Camargue conducted in (2016) by the Regional Natural Park of the Camargue Region). These study sites cover a double gradient related to their salinity and hydrological regime, the latter in terms of flooding temporality, allowing for a comprehensive assessment of GHG emissions, soil carbon stocks and accumulation rates across the region. The wetlands also encompassed a range in the degree of human management (Fig. 1, Table 1).

2.1. Study site description and context

The description of the sites is summarised in Table 1. The sampling stations at Les Garcines, Les Cerisières, L'Esquineau, La Fangouse, La Saline, and Baisse Salée are located in ancient palaeochannels of the river (Muller et al., 2008). Garcines and Esquineau are covered by reedbeds dominated by *Phragmites australis*, of which the former continuously receives freshwater while the latter remains mostly unaltered. Cerisières is a bulrush dominated by *Bolboschoenus maritimus* with natural hydrology. Saline was briefly exploited as a salt production pond at the beginning of the 19th century. It is a shallow marsh naturally temporarily submerged, but with some limited uncontrolled artificial freshwater supply. The Baisse salée is a saltwort steppe on the edge of a palaeochannel, naturally flooded for varying duration periods over the winter. The Fangouse is a bulrush marsh located in a longitudinal depression artificially flooded with freshwater in spring and autumn. Le Fangassier is a former coastal lagoon that was transformed into a salt production basin in the 1970s. Salt production was abandoned in 2009 but soil contains a very large stock of salts as a result of its salt

production history. The Vieux Rhône station is an ancient mouth of the Rhône River fed by fresh water from the Rhône. The Vaccarès and Roselière du Vaccarès sampling stations are located on the eastern edge of the Vaccarès lagoon. This central lagoon is largely supplied with water by drainage channels from its catchment area and experiences significant variations in salinity (Charpentier et al., 2005). The Roselière du Vaccarès is located in a reed belt partly disconnected from the lagoon and exposed to high salinity, and shallow submergence with variable duration, depending on fluctuations of water table depth in the lagoon. The two rice fields of Agon Ouest and Agon Nord are located in an ancient paleochannel of the Rhône. Agricultural management of these two rice fields was conducted following the standard practices of the area. Briefly, fields were water seeded during the first week of May and harvested in mid-October. The water management consisted in continuous flooding at 7–10 cm deep from sowing till the end of August. Nitrogen fertilizer was applied at a total rate of 150 Kg N ha⁻¹, split in three applications of 50 kg N/ha each prior to sowing (April), at tillering (early June) and panicle initiation (early July) stages.

2.2. Greenhouse gas emission rates and environmental and soil characterization

Field sampling campaigns were conducted during the growing season, i.e., from April to November, based on the assumption that most of the annual CH₄ is produced during this period (Xu et al., 2014; Gomez-Casanovas et al., 2020; Huang et al., 2024) when the temperatures are above 12 °C (Marsh et al., 2005). Due to several unexpected drawbacks during the development of the study (e.g., COVID-driven logistic limitations and severe drought periods) we finally discarded three wetlands from the GHG monitoring (Table 1).

Gas sampling was conducted using non-steady state gas chambers (Altor and Mitsch, 2008). The characteristics of the chambers as well as the procedure for chamber deployment and field sampling plan are detailed in (Martinez-Eixarch et al., 2018). In brief, the chambers

consisted of a polyvinylchloride (PVC) structure covered by transparent plastic and were equipped with a thermometer to monitor temperature within the chamber during each extraction. To avoid soil disturbance during gas sampling, blocks were installed in the field to support wooden boards to access the chamber. Methane (CH₄) and nitrous oxide (N₂O) concentrations were determined using a THERMO TRACE 2000 (Thermo Finnigan Scientific, USA) gas chromatograph equipped with a flame ionization detector (GC-FID). Analyses of N₂O were carried out using an Agilent 7820 A GC System, (Agilent, USA) equipped with an electron capture detector (GC-ECD). The emission rates of the GHG were obtained from the change of concentration of each gas in each chamber over the 30-min sampling period. During this time gas samples were collected every 10 min from each chamber, resulting in a total of 4 samples per chamber. Gas concentrations obtained from chromatography were calculated based on the ideal gas law. Only significant linear regressions between GHG concentration and time ($P < 0.05$ and $R^2 > 0.70$) were accepted, and non-significant regressions were considered as zero emission rates (Schultz et al., 2023). A total of 214 recordings for emission rate calculation were collected throughout the study period, of which 74 showed a non-significant linear trend with R^2 below 0.70, and thus assigned as zero emission rates. Mean cumulative GHG emitted during each sampling period were calculated. To do so, emissions between two consecutive sampling events were calculated assuming constant emission rates between them and then, they were all summed to calculate the seasonal cumulative CH₄ and N₂O emissions. In addition, global warming potential (GWP) was estimated using CO₂ as a reference gas, and N₂O and CH₄ emissions were converted into CO₂-equivalent. Over a 100-year period, the default GWP of CH₄ and N₂O emissions is 28 and 265 times that of CO₂ emissions, respectively (IPCC, 2014).

$$\text{GWP (CO}_2\text{ - eq)} = 28 \times \text{cumulative CH}_4\text{ emissions} + 265 \times \text{cumulative N}_2\text{O} \quad (1)$$

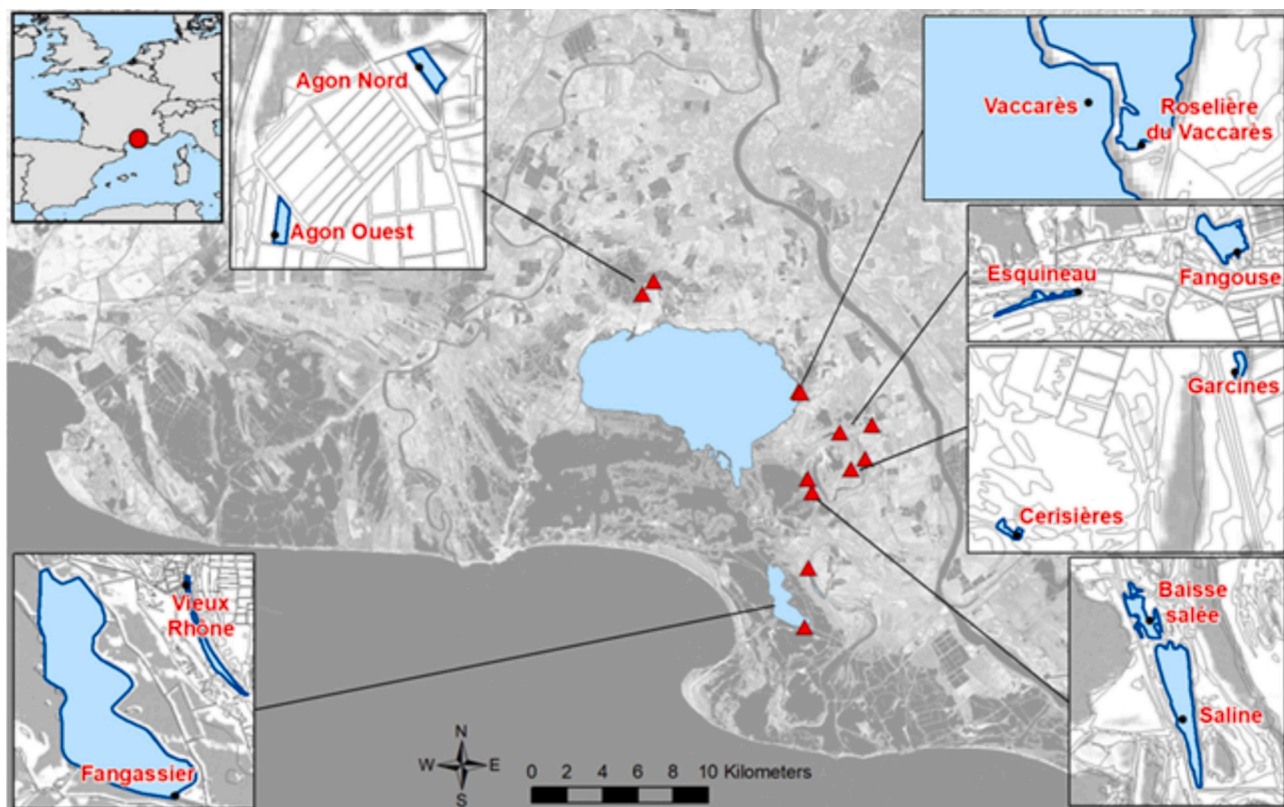


Fig. 1. Location of wetlands and rice fields in Carmargue.

Simultaneously to GHG sampling, soil temperature, water redox potential, conductivity and pH, air temperature and water table depth were recorded using a Hanna HI9126 probe. In addition, percentage of vegetation cover was visually estimated.

Soil samples from each site were taken for soil characterization. Each sample consisted of a composite of 3 subsamples of 30 cm thickness. Soil samples were stored in a fridge at 4 °C until their shipment to external laboratories for analyses.

2.3. Determination of soil organic carbon stocks, sedimentation rates and carbon accumulation rates

One sediment core per site was taken in the summer of 2020 using a steel corer sampler. Each core was approximately 1 m long (diameter: 8 cm). The cores were immediately transferred to a trough, wrapped in cellophane, and taken back to the laboratory for freezing. The compaction of the sediment was measured for subsequent correction of the estimates of the sedimentation rates when necessary (Glew et al., 2001).

Soil cores were sliced each 1 cm for the first 20 cm, and every 2 cm below. The samples were dried at 105 °C to constant weight and subsampled for further analyses. Sub-samples along each core were ground and sent to Edith Cowan University (Perth, Australia) for ²¹⁰Pb analyses. The Pb-210 method was used to determine the accumulation rate of sediments and carbon. The concentrations of ²¹⁰Pb along each core were determined by analysing its decay product ²¹⁰Po in equilibrium by alpha spectrometry after adding ²⁰⁹Po as an internal tracer, digestion in an acid medium using an analytical microwave and plating of the polonium isotopes onto silver disks (Sanchez-Cabeza et al., 1999). Several samples from each core were measured by gamma spectrometry to determine the concentrations of ²²⁶Ra. The concentrations of excess ²¹⁰Pb used to obtain the age models were determined as the difference between total ²¹⁰Pb and ²²⁶Ra (supported ²¹⁰Pb). Sedimentation rates were estimated where possible (i.e., unless mixing dominated the

profile) using the Constant Flux: Constant Sedimentation (CF:CS) and Constant Rate of Supply (CRS) models (Krishnaswamy et al., 1971; Appleby and Oldfield, 1978; Arias-Ortiz et al., 2018).

Soil organic carbon (SOC) content was analysed along each core, with higher resolution for organic carbon (OC) in the top 30 cm. SOC was measured by acidifying 1 g of ground sample with hydrochloric acid (4 % HCl), then centrifuging (3400 rpm, 5 min), and removing the supernatant with acid residues by pipette, before washing with Milli-Q water, centrifuging and again removing the supernatant by pipette. The residual samples were re-dried and weighed, and then encapsulated for analysis at the UH-Hilo Analytical Facilities (University of Hawaii, Hilo, USA) using a Costech Elemental Analyzer. SOC stocks are reported as cumulative stocks for the upper 20 and 100 cm of each core. Organic carbon accumulation rates were calculated by multiplying the OC concentration by the mass accumulation rates.

2.4. Assessment of the effect of wetland management on carbon dynamics

In order to assess the effect of the intensity of management on carbon dynamics of wetlands, and thus their carbon sink capacity, we created a categorical variable based on the intensity of management implemented over the last decades with three levels to which a numerical value was assigned (Table 1): **2** – high (presence of cattle and/or altered hydrological cycle during summer time when the capacity to alter carbon dynamics peaks); **1** – medium (presence of cattle and/or altered hydrology during winter, with less capacity to alter carbon dynamics); and **0** – low or absent (current absence of wetland management).

An offset ratio was calculated to assess how much carbon sequestered in the soil is offset by carbon emitted into the atmosphere in form of CH₄: SOC accumulated over the last 40 years divided by C annually emitted as CH₄. Cumulative CH₄ emissions annually emitted in each wetland were estimated by multiplying the mean emission rates (units in mg m⁻² day⁻¹) by the total number of days of the sampling period under the assumptions of 1) constant emission rates and, 2) no CH₄ was emitted

Table 1

Wetlands selected for monitoring of greenhouse gas emissions and determination of soil organic carbon stocks.

Site	Hydrology	Habitat type	Dominant vegetation	Salinity type	Pore water conductivity (mS cm ⁻¹)	Management degree	Type of management
Agon-Nord	Permanent	Rice field	<i>Oryza sativa</i>	Subsaline	5.5 ± 0.2	High (2)	Rice cultivation with summer permanent freshwater flooding
Agon-Ouest	Permanent	Rice field	<i>Oryza sativa</i>	Subsaline	1.5 ± 0.1	High (2)	Rice cultivation with summer permanent freshwater flooding
Esquieuau	Temporary	Reedbed	<i>Phragmites</i>	Subsaline	3.5 ± 0.8	Medium (1)	Presence of cattle.
Garcines	Temporary	Reedbed	<i>Phragmites</i>	Subsaline	3.2 ± 0.2	Medium (1)	Hydrology dependent on canals, continuously receiving freshwater from canals. No presence of cattle for the last 40 years.
Vieux Rhône	Permanent	Meadow	<i>Potamogeton, Rupia</i>	Hyposaline	8.2 ± 0.6	High (2)	Intentionally flooded with freshwater during summer for hunting.
Fangouse [§]	Temporary	Bulrush	<i>Scirpus maritimus</i>	Hyposaline	10.9 ± 2.9*	Medium (1)	Intentionally flooded with freshwater in spring and autumn
Cerisières [§]	Temporary	Bulrush	<i>Scirpus maritimus</i>	Hyposaline	6.9 ± 1.2 [§]	Low (0)	Presence of cattle. Natural hydrological cycle with submergence from late autumn to spring
Vaccarès roselière	Temporary	Reedbed	<i>Phragmites</i>	Mesohaline	36.2 ± 3.2	Medium (1)	The lagoon is largely supplied with water by drainage channels and experiences significant variations in salinity
Saline	Temporary	Meadow	<i>Ruppia cirrhosa, Potamogeton pectinatus</i>	Mesohaline	36.1 ± 3.3	Low (0)	Currently, no management. Artificially supplied with fresh water through leaks in the irrigation networks and/or for agricultural (livestock) or hunting purposes.
Vaccarès	Permanent	Meadow	<i>Zostera noltei</i>	Mesohaline	40.1 ± 0.8	Medium (1)	The lagoon is largely supplied with water by drainage channels and experiences significant variations in salinity
Baisse salée [§]	Temporary	Gasswort salt meadow	<i>Arthrocnemum glaucum</i>	Mesohaline	32.7 ± 2.7	Low (0)	Absent
Fangassier	Temporary	Saltpan	No vegetation	Hypersaline	146.1 ± 5.3	Absent	Former coastal lagoon transformed into a salt production basin in the 1970s and abandoned in 2009

out of the growing season. This offset ratio could only be calculated for wetlands wherein CH₄ emissions were monitored and the estimation of carbon accumulation over the last 40 years was possible, namely: Vieux Rhône, Garcines, Esquineau, Roselière du Vaccarès and the rice field Agon-Ouest.

2.5. Statistical analyses

Principal component analysis (PCA) was conducted to explore the patterns of association between soil physicochemical variables, water table depth and GHG emission rates. The Kaiser–Meyer–Olkin's (KMO) measure of sampling adequacy was used to assess the usefulness of the PCA. KMO ranges from 0 to 1 and should be above 0.5 if variables are sufficiently interdependent for the PCA to be useful (Tabachnick et al., 2001).

We employed a Generalized Linear Mixed Model (GLMM) to investigate the relationship between CH₄ emission rates and key environmental factors within wetland ecosystems. These factors included vegetation cover, soil temperature, pore water redox potential, pore water conductivity, and water table depth. CH₄ emission rates were used as the response variable ($n = 97$). The first-term interactions between the water table depth and *i*) soil temperature, *ii*) pore water conductivity, and *iii*) pore water redox potential were included as interacting covariates. The vegetation cover was not included in the model as it is highly correlated with the water conductivity ($r > 0.7$) and thus its inclusion would entail potential multicollinearity issues. Finally, the plot identity was included as a random effect and a tweedy distribution of errors used, which is recommended for zero-inflated, positive skewed data.

To assess the influence of human management practices on wetlands, we analysed the relationship between soil organic carbon (SOC) stocks in the topsoil (0–20 cm deep) and the management intensity. We then compared the SOC among the three types of wetlands (i.e., highly-, medium-, and lowly-managed wetlands) by applying a Wilcoxon non-parametric test. The GLMM was carried out using the glmmTMB package developed by Brooks et al. (2017) and the emmeans package introduced by Lenth (2022). The Wilcoxon test was applied using the Wilcoxon-test cite function implemented in the rstatix R package (Kas-sambara, 2023). All the analyses were conducted with statistical Kas-sambara (2023) in R (R Core Team, 2022).

3. Results

3.1. Environmental traits, salinity and hydrology regime of wetlands and rice fields

Soil traits of wetlands is summarised in Table 2. Briefly, the wetland

soils exhibited a near-neutral to slightly alkaline pH range, had high calcium carbonate content, and primarily consisted of clayey and silty textures. SOC content ranged from 0.34 % to 4.6 % and soil sulphate content was variable, ranging from 13 mg kg⁻¹ to 2050 mg kg⁻¹.

Based on the hydroperiod, wetlands were classified as permanently or temporarily flooded (Table 1). It should be noticed that Fangouse, Cerisieres, and Baisse Salée are wetlands with submerged periods typically occurring from winter to spring. However, due to exceptionally dry conditions during the study period, these wetlands remained unflooded for most of the observation period (Fig. 2).

Wetlands were categorized based on mean pore water conductivity (Table 1), following the methodology outlined by Herbert et al. (2015). Water conductivity displayed variations during the study period, primarily in response to hydrological dynamics resulting from either natural (i.e., seasonal fluctuations driven by autumn-winter rainfall and spring-summer drawdown and interannual variations related to rainfall) or management (intentional flooding with freshwater) (Fig. 2).

Pore water redox mostly remained above the critical range (–100 to –210 mV, Fig. 2), in which methanogenesis is initiated (Wang et al., 1993) whereas it remained below this critical threshold in Vieux Rhône. Cover vegetation varied temporally, peaking from August to October (data not shown). Vegetation was absent in the saltpan Fangassier.

3.2. Greenhouse gas emissions

In natural wetlands, the mean CH₄ emission rate (Fig. 3A, B) was 5.8 ± 1.4 mg CH₄ m⁻² h⁻¹ which was comprised within a wide range between – 87.0 and 131.0 mg CH₄ m⁻² h⁻¹. Vieux Rhône and Garcines (Fig. 3B) showed the largest mean rates, 31.0 ± 9.8 mg CH₄ m⁻² h⁻¹ and 22.2 ± 7.4 mg m⁻² h⁻¹, respectively, while the remaining emitted on average <0.5 mg CH₄ mg m⁻² h⁻¹ (Fig. 3A). Temporal variation of CH₄ emissions was consistent across the sampling periods in most study sites except in Garcines and Esquineau. In Garcines, emission rates during the first two sampling periods were low (-1.2 ± 1.0 and 3.1 ± 2.5 mg CH₄ m⁻² h⁻¹) but then they increased up to 53.9 ± 14.1 mg m⁻² h⁻¹ in the 2021 sampling period, coinciding with the managed flooding. By contrast, CH₄ emission rates in Esquineau were higher in the 2019 sampling period (4.0 ± 0.9 mg m⁻² h⁻¹) than in the following ones, when negative fluxes were found (chronologically: -0.8 ± 1.4 and -7.1 ± 2.6 mg CH₄ m⁻² h⁻¹). Low N₂O emissions were found in both rice fields (Fig. 3C): around zero or negative in Agon-Nord (mean: -0.002 ± 0.005 mg m⁻² h⁻¹) and positive in Agon-Ouest (mean: 0.010 ± 0.011 mg m⁻² h⁻¹). A peak of emissions was observed in both fields in July, after the third fertilization, reaching 0.008 ± 0.02 mg N₂O m⁻² h⁻¹ and 0.07 ± 0.04 mg N₂O m⁻² h⁻¹. In natural wetlands, the mean emission rate was 0.005 ± 0.005 mg m⁻² h⁻¹, with values ranging from – 0.5 to 0.9 mg m⁻² h⁻¹ (Fig. 3C, D).

Table 2

Soil traits of wetlands and rice fields monitored in the study. Abbreviations: SOM, soil organic matter; TC, total carbon; TOC, total organic carbon; CaCO₃, carbonate.

Site	SOM (%)	TC (%)	TOC (%)	CaCO ₃ (%)	N-kjedahl (%)	Bulk density (kg/m ³)	Sulphates (mg kg ⁻¹)	Clay (%)	Silt (%)	Sand (%)	Texture
Esquineau	3.5	6.1	2.0	27.8	0.18	837	27	42.1	38.4	19.5	Clay
Garcines	1.4	4.6	1.0	30.3	0.09	838	13	46.4	34.3	19.3	Clay
Fangassier	2.8	4.4	0.9	28.6	0.10	923	2050	23.1	48.4	28.5	Loam
Vaccarès-roseliere	2.6	6.1	1.8	35.8	0.10	801	200	38.1	38.4	23.6	Clay loam
Saline	0.9	5.2	0.7	37.5	0.07	1007	370	52.1	34.3	13.6	Clay
Vaccarès	0.5	4.2	0.3	32.5	<0.02	984	150	6.3	14.1	79.5	Loamy sand
Vieux Rhône	1.5	5.5	1.1	36.5	0.09	912	22	58.2	40.2	1.7	Silty clay
Cerisieres	2.0	5.3	1.3	32.6	0.19	1091	68	42.5	42.4	15.1	Silty clay
Baisse salée	1.0	4.5	0.4	34.8	0.08	731	419	58.2	32.6	9.2	Clay
Fangouse	5.5	8.5	4.6	32.9	0.53	835	218	32.1	30.3	37.6	Clay loam
Rice field-Agon Ouest	1.5	5.4	0.9	37.9	0.09	814	38	42.2	46.3	11.5	Silty clay
Rice field-Agon Nord	0.5	4.8	0.5	36.4	0.03	733	44	22.3	50.2	27.5	Silt loam

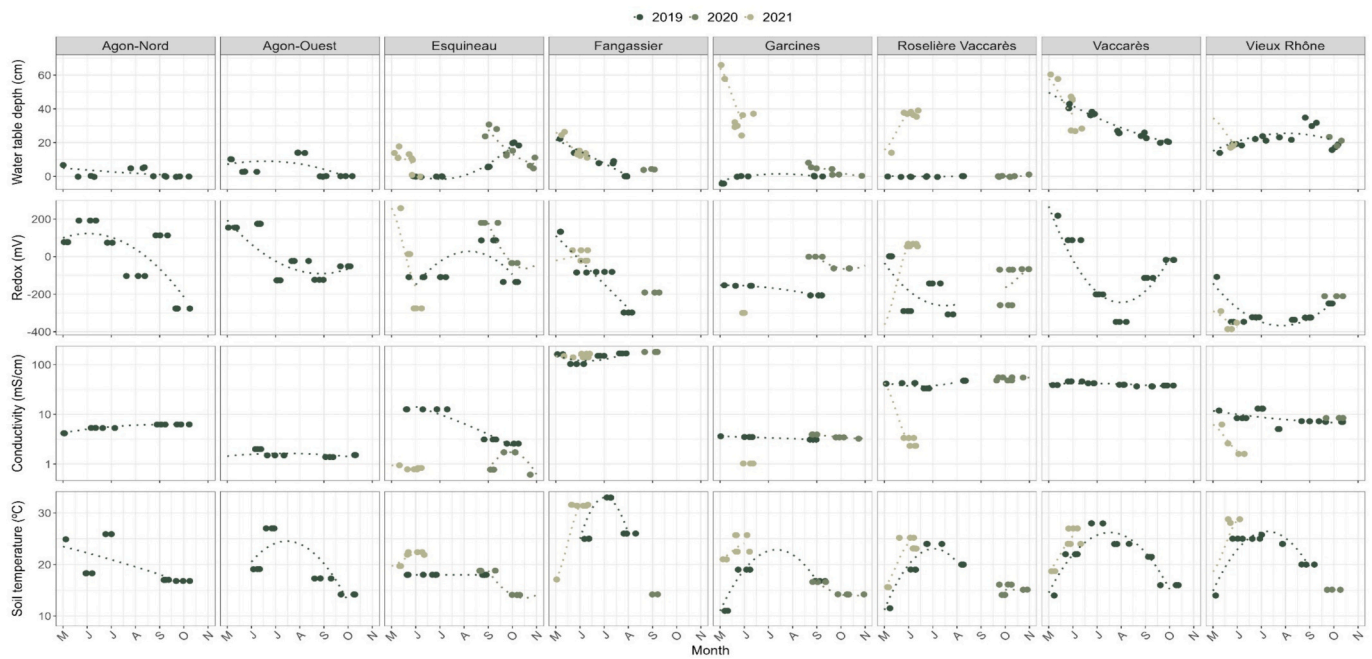


Fig. 2. Temporal variation of the environmental variables of the wetlands and rice fields over the three sampling periods (years 2019, 2020 and 2021). Note that the scale in conductivity is logarithmic.

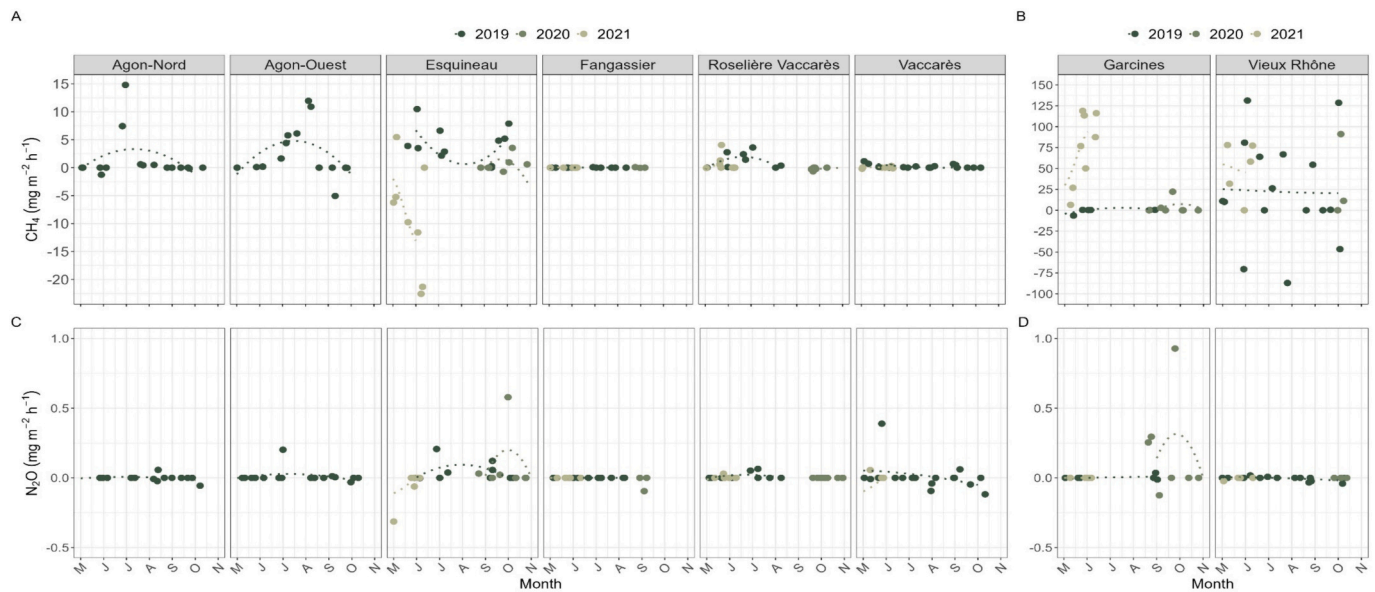


Fig. 3. Temporal variation of CH₄ and N₂O emission rates over the three sampling periods (years 2019, 2020 and 2021). A, C) show CH₄ emission rates and N₂O emissions rates, respectively of rice fields (Agon-Nord and Agon-Ouest), Esqueineau, Fangassier, Roselière du Vaccarès and Vaccarès. B, C) show CH₄ emission rates and N₂O emissions rates, respectively of Garcines and Vieux Rhône. Note that the Y-axis scale in A, C and B, D are different.

The cumulative emissions of CH₄, N₂O as well as the global warming potential (GWP) are illustrated in Fig. S1. Cumulative CH₄ (Fig. S1A) and N₂O (Fig. S1B) emissions ranged from -139.6 to 289.4 g CH₄ m⁻² (both observed in Vieux Rhône) and between -0.3 (Esqueineau) to 0.9 (Garcines) g N₂O m⁻². The overall global warming potential ranged from -3923.0 to 8068.5 g CO₂-eq m⁻² (both observed in Vieux Rhône).

The PCA of the environmental variables and CH₄ emissions indicated that 43.2 % of the variability was explained by the first two components (Fig. 4). The first component explained 23.2 % of the variation and described a positive correlation between vegetation cover and CH₄ emissions, which were negatively correlated to water conductivity and water redox. The second component described 20 % of the variation and

showed a positive correlation between water table depth, soil temperature and CH₄ fluxes, which were all negatively correlated to porewater redox potential and N₂O emissions.

We used a GLMM to analyse the relative effect of the main environmental factors on CH₄ emissions. The analysis revealed a significant effect of water conductivity ($Z = -1.9, P = 0.05$), water table depth ($Z = 2.3, P < 0.01$), water redox ($Z = -4.1, P < 0.001$), soil temperature ($Z = 3.2, P < 0.001$) and the interactions of water table depth with water redox ($Z = 3.1, P < 0.001$) and marginally the interaction of water table with soil temperature ($Z = -1.8, P = 0.06$) (Fig. 5). Under reductive conditions, CH₄ emission rates were higher in shallow than in deeper layers and increased exponentially. Soil temperature enhanced CH₄

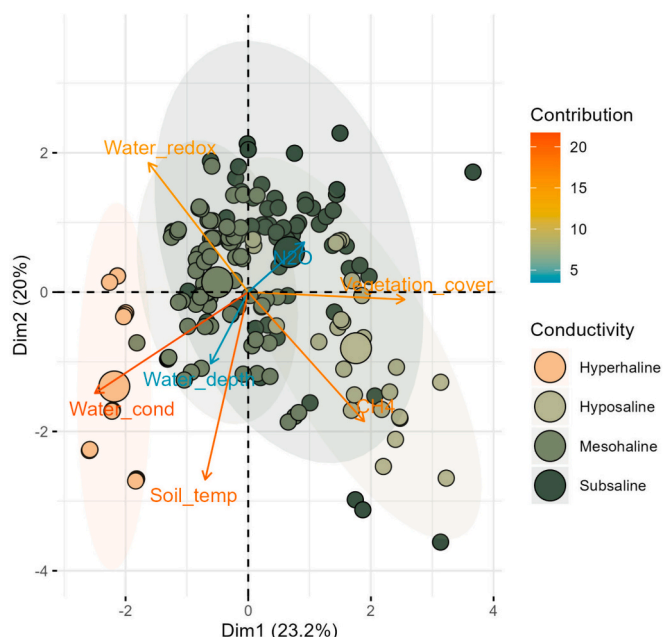


Fig. 4. Principal component analyses (PCA) of environmental variables and CH₄ emissions. Arrows represent factor loadings of the variables, and the scores show the distribution of the plots grouped by conductivity type classified as: hypersaline (Fangassier), mesohaline (Roselière du Vaccarès and Saline), hyposaline (Vieux Rhône) and freshwater (rice fields, Garcines and Esquineau).

emissions with shallower water table compared to deep layers whereas the opposite was found when the temperature was below 25 °C. Regarding conductivity, CH₄ emissions exhibited an upward trend with decreasing conductivity. However, when water conductivity dropped below ca. 30 mS cm⁻¹, CH₄ emissions increased more rapidly as the water layers became deeper, whereas no differences were observed for water conductivity levels higher than 30 mS cm⁻¹.

3.3. SOC stocks and accumulation rates

SOC stock integrated for the upper 100 cm ranged from 17 to 90 Mg OC ha⁻¹ (Fig. 6) and followed a salinity gradient with the largest stocks (from 70 to 90 Mg OC ha⁻¹) found in the low-salinity wetlands and the lowest stocks (< 40 Mg OC ha⁻¹) in the mesohaline and hypersaline wetlands.

The analyses of the relationship between topsoil (0–20 cm deep) SOC stock and the management intensity (Fig. 7) revealed a significant effect of wetland management ($Z = 2.35, P = 0.02$; $Z = 1.81, P = 0.07$ for medium and high intensity management, respectively). Unmanaged wetlands contained lower topsoil SOC stocks (< 17 g OC m⁻²) than those managed (from 18 to 46 g OC m⁻²) with the exception of Vaccarès site, that presented the lowest stock (3 g OC m⁻²). The intensive water wave erosive processes to which this site is subjected may prevent the accumulation of SOC. Because such an effect might have interfered with the assessment of the effect of human activity on SOC accumulation, Vaccarès was removed from the analyses. As a result, the effect of management on topsoil SOC stocks became more significant ($Z = 4.93, P \leq 0.0001$; $Z = 2.91, P < 0.01$).

Rates of sediment and carbon accumulation for the last 40 years could only be estimated in 7 out of the 12 wetlands, since the other five sites presented evidence of mixing of the upper layers (Agon-Nord, Fangouse, Baisse Salée) or lack of net sedimentation (Vaccarès lagoon), which could be related to erosion (Supplementary data set S1). In these 7 wetlands, the maximum reliable sedimentation rates applicable was up to 40 years. Thus, where dating was possible (Esquineau, Agon-Ouest, Saline, Cerisières, Vieux Rhône, Garcines and Roselière Vaccarès) the mean sediment accumulation rate was $1.8 \pm 1.3 \text{ mm yr}^{-1}$ (between 0.49 ± 0.05 in the reedbed Esquineau and $4.3 \pm 1.3 \text{ mm yr}^{-1}$ in the rice field Agon-Ouest). Carbon accumulation rates ranged from $22.5 \pm 3.9 \text{ g OC}$

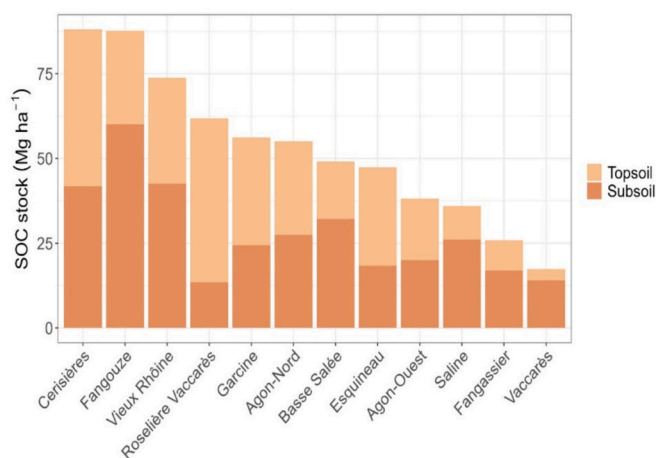


Fig. 6. Stocks of organic carbon accumulated in the 100 cm-deep soil profile, the topsoil (0–20 cm) and subsoil (20–100 cm).

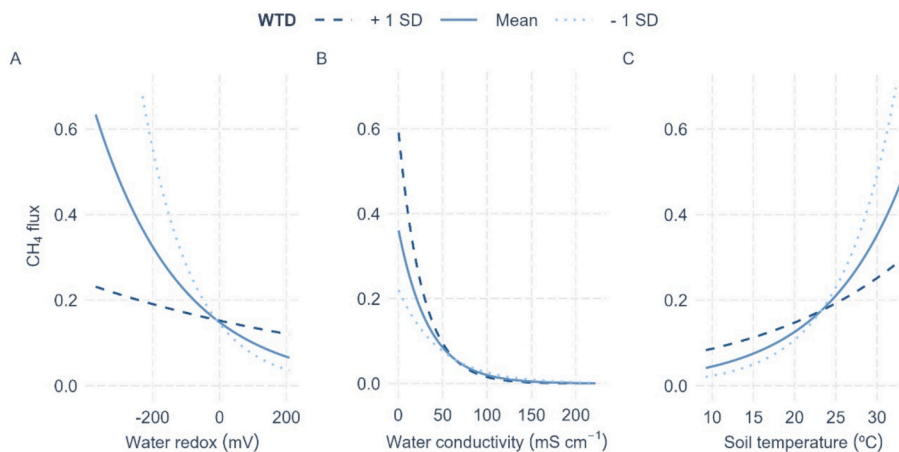


Fig. 5. Interaction effect of water table depth with water redox, water conductivity and soil temperature on CH₄ emissions. Linear regressions between the mean and the mean ± 1 standard deviation of water table depth (WTD) and CH₄ emissions along the recorded values of water redox (A), water conductivity (B) and soil temperature (C) are shown.

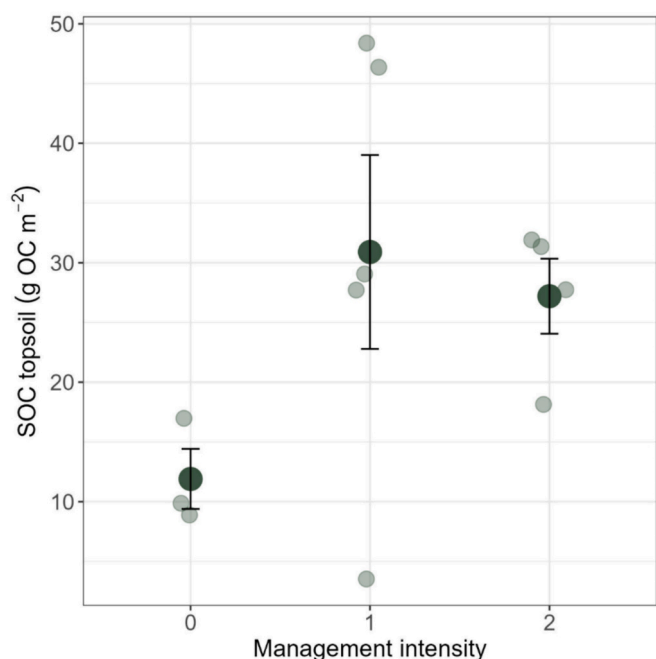


Fig. 7. Relationship between management intensity of the wetlands and topsoil (0–20 cm) SOC stock. Management intensity categories indicate: **0** – low or absent (current absence of wetland management); **1** – medium (presence of cattle and/or altered hydrology during winter, with less capacity to alter carbon dynamics); **2** – high (presence of cattle and/or altered hydrological cycle during summer time when the capacity to alter carbon dynamics peak). Small semi-transparent points indicate topsoil SOC stock for each field. Large solid points and error bars indicate the estimated topsoil SOC stock and the standard errors provided by the GLMM, respectively.

$\text{m}^{-2} \text{yr}^{-1}$ at the Saline marsh to $64 \pm 5 \text{ g OC m}^{-2} \text{yr}^{-1}$ at Cerisières. It is remarkable the high carbon accumulation rate in the rice field Agon-Nord, $53 \pm 17 \text{ g OC m}^{-2} \text{yr}^{-1}$, which is comparable to those in wetlands with the highest rates.

4. Discussion

4.1. Greenhouse gas emissions

The main environmental driving forces of CH_4 emissions were water conductivity, soil temperature, water table depth and pore water redox. Therefore, despite the large variability observed across the wetlands in the Camargue (between -87.0 and $131.0 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$), CH_4 emissions were restricted to subsaline or hyposaline wetlands during the flooding periods. By contrast, mesohaline and hypersaline wetlands emitted at rates below $1.0 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$, regardless of the water regime. This threshold is aligned with the global median of $0.15 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$ estimated in shallow vegetated coastal systems by Al-Haj and Fulweiler (2020) and falls within the range of CH_4 emissions in temperate saltmarshes reported in North Carolina-USA (Shiau et al., 2016), and Mediterranean saltmarshes in Europe (Burgos et al., 2015; Huertas et al., 2017; Huertas et al., 2019; Morant et al., 2020; Canning et al., 2021) and in China (Ye et al., 2016).

Among the subsaline and hyposaline wetlands, the largest CH_4 emissions were found in Vieux Rhône ($31.0 \pm 9.8 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$) and Garcines ($53.9 \pm 14.1 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$). These rates are close to the maximum global medians that ranged from 26.7 to $62.9 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$ Al-Haj and Fulweiler (2020). In rice fields, mean CH_4 emission rates were $1.7 \pm 0.7 \text{ mg m}^{-2} \text{h}^{-1}$ which were lower than those reported in other European rice growing areas such Ebre Delta ($3.3 \pm 0.1 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$; Martínez-Eixarch et al. (2018)), southern Spain (range: 2 – $14 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$; Seiler et al. (1983)) and Italy ($11.4 \text{ mg m}^{-2} \text{h}^{-1}$;

Mejjide et al. (2011)).

Methane emissions primarily occurred within wetlands and rice fields when specific conditions converged: low water conductivity ($< 10 \text{ mS cm}^{-1}$), high soil temperature ($> 20 \text{ }^\circ\text{C}$) and submerged soil with reducing conditions (redox $< 150 \text{ mV}$). Extended periods of permanent flooding induced anoxia in the soil, creating an environment conducive to methanogenic activity. However, water conductivity, closely associated with sulphate content in coastal wetlands (Schultz et al., 2023), acted as an inhibitor of CH_4 emissions, since sulphate-reducing bacteria outcompete methanogens (Poffenbarger et al., 2011). When water conductivity remained below 10 mS cm^{-1} and was coupled with high temperatures ($> 20 \text{ }^\circ\text{C}$) primary production was likely stimulated. Primary production is positively related to CH_4 production (Huertas et al., 2019; Zhang et al., 2022) and CH_4 plant-mediated emission (Laanbroek, 2010). Despite flooding conditions being necessary for CH_4 emissions, the significant interaction of water table depth with both water redox and soil temperature indicated that deep-water layer acted as a buffer of CH_4 emissions under either high soil reducing conditions (i.e., more negative redox values) or high soil temperature.

Unaltered coastal wetlands in summertime experience a decrease in water table depth alongside an increase in water conductivity. This combined effect maintains low CH_4 emissions, which might otherwise be exacerbated by the high temperatures. Vieux Rhône is a permanently flooded and highly productive wetland artificially supplied with freshwater during summer for hunting purposes, thus disturbing the natural temporal salinity and hydrology variation. This management leads to the CH_4 -boosting combination of low conductivity and flooding under high temperature. The exacerbating effect of managed freshwater flooding on CH_4 emissions in low-salinity natural wetlands was also apparent in the Garcines reedbed. During the first two sampling periods, this reedbed was dry or soil saturated because of the summer drought, resulting in minimal or negligible CH_4 emissions. However, during intentional flooding, CH_4 emissions sharply increased to $32.2 \pm 9.8 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$. Hence, our study highlights that altering the natural temporal hydrology and salinity patterns of hyposaline Mediterranean natural wetlands through freshwater flooding can significantly increase CH_4 emissions.

Nevertheless, a markedly distinct pattern emerged in Esquineau, an adjacent reedbed to Garcines, both sites sharing similar soil characteristics and plant community (Tables 1 and 2). The main divergence in these two wetlands on CH_4 dynamics can be attributed to differences in their exposure to human-induced hydrological changes and the grazing regime. Esquineau periodically dries out in summer for several weeks, aligning with the natural hydrology, and it is exposed to grazing. By contrast, Garcines is continuously supplied with freshwater leaked from the nearby canals and unexposed to grazing. During the period when the study was conducted, these two wetlands had a similar hydrological pattern so that they both dried out rapidly in spring 2019, experienced a marked summer dry spell in 2020, and were subsequently artificially flooded until summer 2021. In Esquineau, CH_4 emissions were only detected during the first dry sampling period at rates approximately one-tenth lower than those observed in Garcines. Furthermore, while the large aforementioned CH_4 emissions in Garcines were confined to the managed flooding period, Esquineau displayed CH_4 uptake ($-7.2 \pm 2.6 \text{ mg CH}_4 \text{ m}^{-2} \text{h}^{-1}$) during the same flooded period. Anaerobic CH_4 methanotrophy is an important process in coastal freshwater and saltmarsh sediments (Segarra et al., 2013), particularly nitrite/nitrate-dependent microbial CH_4 oxidation (n-DAMO), potentially becoming an important sink of CH_4 . Nitrogen enriched marshlands such as Esquineau, with twice as soil N content as Garcines (Table 2), likely because of the presence of cattle, are prone to harbour this metabolic pathway offering a plausible explanation for both the CH_4 uptake during the flooding period and the lower CH_4 emissions compared to its analogous reedbed, Garcines. However, it should be noted that this pathway remains largely unexplored, so our hypothesis should be further explored. In addition to Esquineau, remarkable negative CH_4 rates

around $-75 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$ were observed in Vieux Rhône during the 2019 sampling period (Fig. 3B) which is aligned to the ranges of annual uptake CH_4 fluxes between 2.0 and $75.26 \text{ mg m}^{-2} \text{ h}^{-1}$ reported by Yang et al. (2018).

Rice fields emitted less CH_4 than the natural low-salinity wetlands, despite receiving significant freshwater inputs throughout the growing season. The development of paddy soil is driven by specific soil management practices such as soil labouing (i.e., ploughing, puddling, and levelling of soil surface), mineral or organic (including crop residue incorporation into the soil) fertilization. These agronomic practices induce changes of oxic and anoxic conditions in the soil leading to variations in reduction and oxidation (redox) reactions (Cheng et al., 2009). Soil redox in rice fields mostly remained either positive or in the upper range (-100 to -150 mV) for methanogenesis (Wang et al., 1993). In addition, soil sulphate concentration, which inhibits methanogenesis (Poffenbarger et al., 2011) doubled that from Garcines and Vieux Rhône. Therefore, the higher ranges of soil redox and higher soil sulphate content in rice fields may explain the lower CH_4 emissions than their natural counterparts.

Our study indicates that wetlands in the Camargue have the capacity to either act as sinks or sources of N_2O , a finding consistent with previous research by Foster and Fulweiler (2016) and reviewed by Murray et al. (2015). N_2O consumption is favoured by high soil moisture, low mineral N and high soil C (Majumdar, 2013), conditions usually met in wetlands and rice fields. Despite the observed low rates, high N_2O emissions have been reported in other wetlands (Lienggaard et al., 2013; Kasak et al., 2022). Hence, considering the potent warming capacity of this molecule, approximately 265 times greater than that of CO_2 , monitoring of N_2O in wetlands should be conducted.

The ranges of cumulative CH_4 , N_2O emissions observed in this study (-139.6 to $289.4 \text{ g CH}_4 \text{ m}^{-2}$; -0.3 to $0.9 \text{ g N}_2\text{O m}^{-2}$) agree with those reported by Yuan et al. (2021) and references therein.

4.2. Soil organic carbon stocks and accumulation rates

The organic carbon stocks in the upper meter in the Camargue are low (17 to 90 Mg OC ha^{-1}) and comparable to those found in other coastal wetlands (Serrano et al., 2019; Vaughn et al., 2021; Bai and Cotrufo, 2022). Similarly, the range of carbon accumulation rates over the last 40 years (21 to $64 \text{ g OC m}^{-2} \text{ yr}^{-1}$) were slightly lower than the $55 \pm 2 \text{ Mg OC ha}^{-1} \text{ yr}^{-1}$ in tidal marshes in Australia (Macreadie et al., 2017; Serrano et al., 2019), and fall within the lower range (14 – $435 \text{ g OC m}^{-2} \text{ yr}^{-1}$) of those reported in the US- North Carolina (Miller et al., 2022) and in Spain, in the Ebro Delta (Fennessy et al., 2019). There are several plausible reasons for these relative low carbon sequestration rates and SOC stocks. The temporary submergence with summer drying limits plant production and enhances the degradation of organic matter (Bai and Cotrufo, 2022), thus limiting efficient C storage capacity. The summer drying in the Camargue is the natural result of the combination of shallow wetlands and high-water deficit since evapotranspiration is almost 3 times greater than average rainfall (around 1500 mm and 600 mm respectively: Tour du Valat meteorological station, unpublished data). In addition, the Camargue conserves more surface of salt marshes (often with hypersaline soils) with less hydrological alteration than other similar systems such as the Ebro Delta. Saline wetlands disconnected from the sea and subject to a significant water deficit can quickly increase salinity and reach very high levels, severely limiting primary production. This is, for instance, the case in the Saline and Fangassier marshes and the Baisse salée steppe. The highest SOC stocks ($>75 \text{ Mg OC ha}^{-1}$) and accumulation rates ($>50 \text{ g OC m}^{-2} \text{ yr}^{-1}$) were observed in the hyposaline environments. The SOC stock in the topsoil in the Camargue wetlands is significantly influenced by human management practices carried out over the past few decades. Altered hydrology of the wetlands based in large inputs of freshwater in low-salinity wetlands increased the accumulation of SOC in the topsoil. This phenomenon can be attributed to the effect of increased allochthonous nutrient and

organic matter input in these already high primary productive systems. In the case of Vieux Rhône and Garcines, these inputs come from freshwater supplied by either the river or irrigation canals, while in the rice fields and Esquineau, they result from fertilization and livestock-related nutrient input, respectively.

4.3. Soil carbon sequestration and CH_4 offsets: management implications on carbon sink capacity of coastal natural wetlands in the Camargue

Coastal wetlands represent an important blue carbon sink with implications for climate change mitigation. The overall sink capacity of the wetlands depends on the balance between soil carbon sequestration and GHG emissions, mainly CH_4 . Our study confirms that both SOC storage capacity and CH_4 emissions decline with salinity, so that mesohaline wetlands have low CH_4 emissions but also less SOC stocks than low-salinity wetlands. By contrast, low-salinity wetlands are highly productive systems with the dual effect of providing SOC storage potential while stimulating CH_4 emissions, especially in summertime when the high temperatures enhance methanogenesis (Fey and Conrad, 2003).

The natural hydrological cycle of Mediterranean coastal wetlands, consisting of summer drought accompanied by increases in conductivity, limits the potential methanogenic activity, thus favouring more carbon being sequestered than emitted. Conversely, in highly managed coastal wetlands with the natural hydrological cycle altered by supplying freshwater in summertime can exacerbate CH_4 emissions, offsetting the capacity of wetlands to sequester carbon, and potentially turning them from sinks to net sources of carbon. In our study this is clearly observed at the Vieux Rhône and Garcines sites. While the ancient mouth of the Rhône River holds relatively large topsoil SOC stocks (31 Mg OC ha^{-1}), it also presents the highest mean CH_4 emissions rate ($31 \pm 10 \text{ mg CH}_4 \text{ m}^{-2} \text{ h}^{-1}$). Soil carbon accumulation rates can be used as a proxy for the net ecosystem carbon balance (Forbrich et al., 2018; Arias-Ortiz et al., 2021) as it represents the balance between carbon inputs (primary production and allochthonous carbon deposition) and outputs (heterotrophic and autotrophic respiration, and carbon export). Concretely, Arias-Ortiz et al. (2021) reported that in non-tidal wetlands, carbon accumulation rates are equivalent to net ecosystem balance. This equivalence is due to estuarine wetlands typically being CO_2 sinks and the negligible lateral carbon export in non-tidal systems such as wetlands in Camargue that have a microtidal range (Rey et al., 2009). Then, if, as a first approximation, we calculate the percentage of carbon annually emitted as CH_4 offsetting the soil carbon sequestration (Nag et al., 2017a, 2017b; Debanshi and Pal, 2022; Schultz et al., 2023), both Garcines and Vieux Rhône act as sources of C since the rate of annual carbon loss as CH_4 is more than twice as high as soil carbon accumulation rate (offset ratio of 270 % and 230 %, respectively). Interestingly, this is not the case of rice fields which presented comparable topsoil SOC stocks (18 and 28 Mg OC ha^{-1}) and C accumulation rates over the last 40 years ($53 \pm 17 \text{ g OC m}^{-2} \text{ yr}^{-1}$ in Agon-Nord) but ca.10-fold less CH_4 emissions than Vieux Rhône and Garcines. As a result, CH_4 emissions in rice fields represented 16 % of the soil carbon annually accumulated leading rice fields to act as sink of carbon. This balance was also found in Mediterranean rice fields in Spain (Belenguer-Manzanedo et al., 2022).

In contrast to low-salinity wetlands, emissions of CH_4 in mesohaline make a relatively smaller contribution to the overall carbon budget. In Roselière du Vaccarès, the freshwater supply through the drainage canals did not cause substantial CH_4 emissions (mean annual rate: $4 \pm 2 \text{ g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$) representing only 6 % of the mean annual accumulation of organic soil carbon ($37 \pm 2 \text{ g C m}^{-2} \text{ yr}^{-1}$) thus becoming a sink of carbon. The offset ratio can be informative of the overall C balance; however, it should be taken carefully because the herein presented cumulative CH_4 emissions were estimated based on monthly sampling whereas more intense sampling frequency might be required for a more accurate estimation of annual emissions. Nevertheless, the balances herein provided should be considered as general estimates. While they reflect the overall trends, the percentages given may not be precisely

accurate because the differing time scales represented by carbon accumulation rates and CH₄ emission, and the interannual variability of the latter.

Over the last 70 years, water management in the Camargue has aimed to increase crop production by reducing the salinity of wetlands, and to reduce or eliminate the summer drought that is so pronounced in the Mediterranean climate that prevails there. As shown by this study, this type of management can lead to very high CH₄ emissions. While reducing GHG emissions is a key issue, maintaining economic activities is equally important, and compromises need to be found between these issues. To minimize the trade-off between climate change mitigation and preservation of cultural activities, we suggest a change in hydrosaline management within protected areas and in areas dedicated to leisure activities, notably hunting. Draining the marshes in summer and re-watering them at the end of the summer would significantly reduce CH₄ emissions by maintaining a slightly higher salinity and avoiding flooding during the hot period when emissions are highest. This approach may lead to changes in biomass and specific vegetation composition, but its impact on these cultural activities is expected to be minimal. It is important to note that this recommendation may not be applicable to rice fields for different reasons. Firstly, rice fields acted as sink of carbon. However, it should be acknowledged that this carbon balance was only measured in one rice field, hence extrapolating it to the entire rice-growing area might not be accurate. Secondly, rice cultivation in the Camargue, conducted under permanently flooded over the 6-month growing season, is a primary economic income in the area and needs to be preserved. The cultivation of rice under flooded conditions is due to the agronomic advantages associated with this practice, namely effective weed control and prevention of salinity stress (Datta et al., 2017). The latter is particularly important in coastal rice fields, such as the rice growing area in the Camargue. Consequently, alterations to this irrigation regime should be thoroughly justified, both in agronomic and environmental terms. Moreover, if deemed appropriate, these alterations should be studied under site-specific conditions prior to implementation. Further work is needed to gain a better understanding of GHG emissions under a more restricted range of hydrosaline conditions, and in partnership with local stakeholders in the search for these management compromises. Climate change and, in particular, the availability of water from the Rhône, now virtually unlimited in the delta but expected to drop drastically with climate change, should also be factors to be considered in the medium term.

5. Conclusions

This study presents the first estimation of SOC stocks, accumulation rates and greenhouse gas emissions in wetlands in the Camargue based on the compilation of data from 12 wetlands representative of the habitats in the area, including rice fields. We did so by assessing the combined effect of environmental and management drivers on the carbon budgets in a highly managed wetland system such as the Camargue. There are some limitations in this study resulting from the sanitary and climatic context in which it was framed. Nevertheless, this project provides the first data on SOC stocks and GHG emissions in the Camargue wetlands and rice fields and identified the conditions that affects these emissions. Beyond their local importance, the results are also useful for calibrating or validating large-scale modelling projects.

Overall, SOC stocks are low compared to those reported in wetlands elsewhere. In most of the studied wetlands, GHG emissions are also low but a few of them emitting large quantities of CH₄. Emissions of CH₄ only occurred in flooded, low-saline wetlands and rice fields whereas minor or negligible emissions were found in mesohaline and hypersaline environments, regardless of the hydrology regime. Conductivity, redox, soil temperature and water table depth were the main drivers of CH₄ emissions. Water table depth acts as a buffer of CH₄ emissions, so that under favourable environmental conditions for CH₄ emissions provided by either high soil reducing conditions or high soil temperature, deeper

water layer reduced CH₄ emissions. The largest topsoil SOC stocks and carbon accumulation rates over the last 40 years are found in the hyposaline wetlands, though large CH₄ emissions in some of them offset the C storage capacity. By contrast, rice fields, and mesohaline wetlands act as sinks of carbon. The knowledge provided by our study is pivotal for enhancing our understanding of carbon dynamics in these wetlands and for better planning their management strategies. Our findings underscore the critical role of low-salinity wetlands in maintaining the balance between soil carbon sequestration and CH₄ emissions. The altered hydrology in the natural marshes needs to be reevaluated and adjusted to preserve the ecosystem service of climate regulation by soil carbon storage provided by coastal wetlands. Based on our findings, summer draining of marshes followed by late-summer re-watering is recommended for the preservation of leisure activities while simultaneously mitigating CH₄ emissions. From a conservation perspective, this hydrological regime corresponds to the Mediterranean climate thus being appropriate for the conservation of indigenous biodiversity. Additional research and collaborative work with local stakeholders are crucial in the pursuit of effective management compromises.

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CRedit authorship contribution statement

Maite Martínez-Eixarch: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Pere Masqué:** Writing – review & editing, Methodology. **Anna Lafratta:** Writing – review & editing, Methodology. **Paul Lavery:** Writing – review & editing, Methodology. **Samuel Hilaire:** Methodology. **Lluís Jornet:** Methodology. **Cyrille Thomas:** Methodology. **Arnaud Boissard:** Methodology. **Néstor Pérez-Méndez:** Writing – review & editing, Visualization, Formal analysis. **Carles Alcaraz:** Writing – review & editing, Formal analysis. **Columba Martínez-Espinosa:** Writing – review & editing. **Carles Ibáñez:** Writing – review & editing, Funding acquisition, Conceptualization. **Patrick Grillas:** Writing – review & editing, Writing – original draft, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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