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# Foregone carbon sequestration loss dominates greenhouse gas budget in mariculture associated with coastal wetland conversion

**Weixin Ding**

wxding@issas.ac.cn

Institute of Soil Science, Chinese Academy of Sciences, Nanjing, China

**Junji Yuan**

Institute of Soil Science, Chinese Academy of Sciences https://orcid.org/0000-0002-8339-699X

**Yanhong Dong**

Institute of Soil Science, Chinese Academy of Sciences

**Junjie Li**

Institute of Soil Science, Chinese Academy of Sciences

**Deyan Liu**

Institute of Soil Science, Chinese Academy of Sciences

**Jian Xiang**

Nanjing Forestry University

**Tiehu He**

Wuhan Botanical Garden, Chinese Academy of Sciences https://orcid.org/0000-0001-8902-5412

**Hojeong Kang**

Yonsei University

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# Abstract

Coastal wetlands represent a disproportionately large global carbon (C) sink. However, they are threatened by the ever-expanding aquaculture and being lost at critical rates. Conversion of coastal wetlands to aquaculture systems has been predicted to result in significant C losses, yet accurate assessments of greenhouse gas (GHG) budgets associated with this major perturbation are rarely available. Here we show that the conversion of *Spartina alterniflora* saltmarsh to mariculture ponds in China induced a dramatic shift from net atmospheric GHG sink (−13.8 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$) to net GHG sources (2.16 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$), creating a full GHG debt of 15.9 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$. The loss of foregone GHG mitigation capacity of saltmarsh makes the largest contribution (86.4%), while only 15.6% of the total debt arises from direct $CO_2$, $CH_4$, and $N_2O$ fluxes in the mariculture ponds. But considering the main drivers of GHG emissions from animal protein production, mariculture has much lower GHG-cost than inland freshwater aquaculture and terrestrial beef, small ruminants, and pork production on a kg $CO_2$eq $kg^{-1}$ protein basis. The low-C mariculture could be further realized by avoiding devastation of vegetated coastal wetlands and minimizing $CH_4$ emission by carrying out in high-salinity waters.


# 1. Introduction

Coastal wetlands are one of the most productive ecosystems and represent an important component of global carbon (C) sinks[1]. They can actively sequester carbon dioxide ($CO_2$) by trapping and burying autochthonous and allochthonous C into sediments and hold up 10–100s times greater rates of C storage per unit area than terrestrial forests[2]. Coastal wetlands only occupy 0.07–0.22% of the Earth's surface but bury 0.08–0.22 Pg C $yr^{-1}$, being equivalent to ~ 10% of the entire net residual land C sink[3,4]. Nevertheless, coastal wetlands emit much lower methane ($CH_4$) relative to freshwater wetlands, and hence have long been recognized as more valuable C sinks for climate change mitigation[5]. However, coastal wetlands are among the most threatened by and vulnerable ecosystems to human activities such as agriculture and aquaculture development, coastal construction, and anticipated climate change and sea level rise[6–8]. Currently, the area of global coastal wetlands decreases at an annual rate of 0.7–7% (ref. [2]). Recent estimates have indicated that 29–50% of global coastal wetlands were lost or degraded during the last four decades[9].

Among all the anthropogenic and natural factors, conversion to aquaculture ponds is the major single cause of coastal wetlands degradation and decline, especially in the Asia-Pacific region[10,11]. With the ever-rising demand for animal-based protein and the dwindling of wild fish stocks, global aquaculture has increased rapidly since the late 1980s (ref. [12]). Nowadays, the contribution of aquaculture to food fish consumption has risen from 19% in 1990 to 52% in 2018 and is expected to increase to 62% by 2030 (ref. [12,13]). The ever-expanding aquaculture accounts for 52% of the 3.6 million ha global mangrove loss since 1980 (ref. [9]). In China, more than 30% of the newly developed mariculture ponds during 1984–2016 were converted from coastal saltmarshes[11]. Upon the steadily increasing demand for fish protein, it is therefore likely that more natural coastal wetlands would be converted to aquaculture ponds in the future[8,10].

The high C densities per unit area of coastal wetlands, coupled with quick losing rates, imply that loss of global coastal wetlands may generate substantial C emissions. Pendleton et al.[14] estimated that total C emissions from conversion and degradation of coastal wetlands were to be 0.15–1.02 Pg $CO_2$eq $yr^{-1}$ globally. Kauffman et al.[15] found that the potential C losses from conversion of coastal wetlands (e.g., mangroves) to shrimp ponds in the Dominican Republic were up to 1,067–3,003 Mg $CO_2$eq $ha^{-1}$. Consistently, Murdiyarso et al.[10] reported that the conversion of mangrove to shrimp ponds in Indonesia resulted in C emission of 0.07–0.21 Pg $CO_2$eq $yr^{-1}$ due to the losses of aboveground and underground C pools. Moreover, aquaculture ponds often receive large amounts of fish feeds and fertilizers to improve production, while only a small portion of these supplied nutrients (11–36% for nitrogen) is converted into fish biomass[16]. The residual organic matter and nutrients could lead to high emissions of methane ($CH_4$) and nitrous oxide ($N_2O$) from aquaculture ponds[17,18]. As $CH_4$ and $N_2O$ are more powerful than $CO_2$ at trapping heat in the atmosphere, a comprehensive scaling of the net emissions from all the three major greenhouse gases (GHG) is necessary to evaluate how aquaculture expansion contributes to global climate change. Particularly, conversion of natural saltmarsh could not only result in the losses of soil and biomass C but also demolish one of their most important ecosystem services, e.g., high rates of $CO_2$ capturing, whereas this foregone GHG mitigation capacity losses and its contribution to the full GHG budget of mariculture has never been scaled in previous studies.

Recently, the updated Intergovernmental Panel on Climate Change (IPCC) reports provided the methodological guidance on GHG emissions from aquaculture systems[19,20]. However, the lack of field direct measurement data increased the uncertainties of the IPCC default emission factors and budget estimates for GHG emissions from aquaculture. For instance, the IPCC Tier 1 $CH_4$ emission factor for saline agriculture and aquaculture ponds has been explored by only 3 published reports from tropical regions[20]. As for the $N_2O$ emission from aquaculture, the IPCC default emission factor and current estimates are also limited by modeling approaches using mathematic reckoning or known as indirect $N_2O$ data[21]. Large variations in $N_2O$ emission factors from aquaculture systems have been found due to the large variability in environmental conditions and yield performance of culturing species[21,22]. Previous studies reported that $N_2O$ production in extensively managed aquaculture ponds was limited by the high dissolved organic C (DOC) concentrations and anaerobic conditions, and the yield-scaled emission factor for $N_2O$ in these ponds was 7.85-time lower than the IPCC default value[17,23]. Therefore, field direct measurements are needed for validating current estimates, specific emission factors development for diverse aquaculture systems, and adoption of effective mitigation strategies.

China's aquaculture industry has experienced rapid development during the past four decades. Nowadays, China alone contributes 58% of global mariculture volume and roughly half of global mariculture area[12,24]. The ever-expanding mariculture has caused substantial loss of coastal wetlands in China and worldwide[9,11]. There is clearly an emerging interest and urgent need for greater appreciation of the GHG emissions incurred during the severe land-use change. Here we quantified the annual fluxes of carbon dioxide ($CO_2$), methane ($CH_4$), and nitrous oxide ($N_2O$) from a natural coastal saltmarsh and three adjacent saltmarsh-converted mariculture ponds within 1 to 5 years, to access the full GHG debt of this typical mariculture mode in China (Supplementary Fig. 1). We also scaled the relative magnitude of each component of GHG from various aquaculture systems (e.g., inland freshwater aquaculture, and brackish shrimp farming and polyhaline

polyculture in coastal regions) and compared emissions from aquaculture to those from livestock production. Findings here will help illuminate the role that aquaculture has in the environmental cost of global food-production systems and explore the potential mitigation strategies for aquaculture.

## 2. Results and discussion

# 2.1 Impacts on $CO_2$ fluxes

Saltmarshes are among the most productive ecosystems in the world with the capacity to store large amounts of C per unit area, referred as "Blue Carbon" [2]. Our high-resolution eddy covariance (EC) measurements of $CO_2$ fluxes revealed that the *S. alterniflora* marsh was a net sink of atmospheric $CO_2$. Daily $CO_2$ fluxes in the marsh exhibited distinct seasonal patterns, with peak $CO_2$ fluxes, e.g., gross primary productivity (GPP), ecosystem respiration (Re), and net ecosystem $CO_2$ exchange (NEE), occurring in summer when vegetation has grown vigorously (Fig. 1a). From late-September, $CO_2$ fluxes gradually declined since both GPP and ER were inhibited by cool temperature. Because of the long green period of *S. alterniflora*, the saltmarsh switched from net $CO_2$ source to net $CO_2$ sink in early April and did not switch back to net $CO_2$ source until December. Over an annual cycle, 65.2 Mg $CO_2$ $ha^{-1}$ (1,778 g C $m^{-2}$) was accumulated as GPP and 47.4 Mg $CO_2$ $ha^{-1}$ (1,293 g C $m^{-2}$) was released as Re in this saltmarsh, resulting in a net uptake of 17.8 Mg $CO_2$ $ha^{-1}$ (485 g C $m^{-2}$) annually (Fig. 2a).

In contrast to *S. alterniflora* marsh, NEE in the mariculture ponds fluctuated between −34.1 and 215.3 mg $CO_2$ $m^{-2}$ $h^{-1}$ and no apparent seasonal variations were observed, except for the pulse of $CO_2$ emission in the initial drainage period (Fig. 1b). On an annual basis, mariculture ponds were net atmospheric $CO_2$ sources ranging from 0.91 to 1.76 Mg $CO_2$ $ha^{-1}$, and the highest $CO_2$ emission was observed in the 1-year old mairculture pond (MP1) (Fig. 2a). The NEE in our ponds compared reasonably with observations from other mariculture systems which also receives feed inputs. Zhang et al.[25] reported an annual $CO_2$ emission of 4.69 Mg $CO_2$ $ha^{-1}$ in a nearby crab-shrimp-clam polyculture system. Recent seasonal measurements from subtropical estuarine shrimp ponds also demonstrated culturing-period $CO_2$ emissions ranging from 0.29 to 0.55 Mg $CO_2$ $ha^{-1}$ (ref. [26]). Aquaculture waters have been documented autotrophic and act as a sink of atmospheric $CO_2$, because primary production of phytoplankton is generally higher than the water-column respiration[26,27]. However, phytoplankton is easily decomposed compared to plant biomass, resulting in minimal retention of primary production. Yang et al.[26] reported a net water-column $CO_2$ fixation of 2.02 Mg $CO_2$ $ha^{-1}$ in a subtropical shrimp pond, which was ~ 1 order of magnitude lower than the $CO_2$ uptake rate in *S. alterniflora* marsh. Therefore, the shift of $CO_2$ sink to source following saltmarsh conversion can be primarily due to the loss of $CO_2$ sequestrating capacity of primary producer. Specifically, prevalence of $CO_2$ efflux in the ponds suggested that water-column $CO_2$ uptake was largely counterbalanced and surpassed by other components of respiration, e.g., soil respiration[26]. It has been estimated that only < 20% of the feed C can be converted to biomass in aquaculture systems, the residuals are buried and then transformed to $CO_2$ and $CH_4$ by microbes[17,28]. However, we found that NEE was significantly higher in MP1 than in the 4-year (MP2) and 5-year (MP3) ponds (Fig. 2a). As C inputs from feeds and fertilizers were similar among ponds, the difference in NEE indicated that the

decomposition of residual fish feed and feces can only be partly responsible for the $CO_2$ emission. Decomposition of SOC, on the other hand, might account more for the $CO_2$ efflux. This can be supported by the significant lower SOC contents in the older ponds relative to MP1 (Table 1). Losses of SOC have been widely reported in wetlands subjecting to reclamation and conversion to other land uses[29,30]. Arifanti et al.[31] found that the SOC mineralization rate over 16 years following mangrove conversion to shrimp ponds was up to 24.5 Mg C $ha^{-1}$ $yr^{-1}$, accounting for 75.0% of total C losses. When coastal wetlands are converted into aquaculture ponds, the top layers of soil are excavated and exposed to oxygen which enhances the susceptibility of SOC to mineralization. Further, operation activities such as aeration, drainage and harvest could also destabilize the SOC, resulting in large amounts of $CO_2$ emission during the initial culturing years[32]. Thereafter, subsequent losses were much slower probably due to the increased proportion of recalcitrant organic C fractions[33,34], as exhibited in the relatively lower NEE in MP2 and MP3.

Table 1
Soil properties in the *Spartina alterniflora* saltmarsh and mariculture ponds.

| Systems | Culture time (year) | Area (ha) | SOC (g C $kg^{-1}$) | TN (g N $kg^{-1}$) | DOC (mg C $kg^{-1}$) | $NH_4^+$ (mg N $kg^{-1}$) | $NO_3^-$ (mg N $kg^{-1}$) | WD (cm) | DO (mg $L^{-1}$) | Salinity (ppt) |
|---|---|---|---|---|---|---|---|---|---|---|
| Saltmarsh | – | – | 15.8 ± 0.2a | 1.04 ± 0.04b | 135 ± 9a | 2.31 ± 0.18b | 0.14 ± 0.03b | 0.12 ± 0.47b | – | 28.2 ± 0.1b |
| MP1 | 1 | 3.87 | 13.5 ± 0.1b | 0.82 ± 0.03a | 47.0 ± 3.8b | 24.4 ± 1.3a | 1.41 ± 0.21a | 88.2 ± 4.0a | 6.83 ± 0.25a | 30.8 ± 0.5a |
| MP2 | 4 | 4.83 | 11.9 ± 0.2c | 0.78 ± 0.01a | 36.3 ± 3.0c | 26.8 ± 1.9a | 1.35 ± 0.23a | 88.9 ± 5.6a | 8.12 ± 0.33b | 29.0 ± 0.4b |
| MP3 | 5 | 4.47 | 11.1 ± 0.2d | 0.77 ± 0.01a | 35.0 ± 3.2c | 28.2 ± 2.0a | 1.23 ± 0.21a | 82.4 ± 5.3a | 8.89 ± 0.31a | 28.6 ± 0.4b |
| *F*-value | – | – | 104.14 | 30.17 | 55.09 | 115.75 | 18.40 | 598.30 | 12.07 | 19.34 |
| *P*-value | – | – | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 | < 0.001 |

MP, mariculture pond; SOC, soil organic carbon; TN, total nitrogen; DOC, dissolved organic carbon; $NH_4^+$, ammonium; $NO_3^-$, nitrate; WD, water depth; DO, dissolved oxygen. Different letters denote significant differences ($P < 0.05$) between groups based on ANOVA followed by Tukey's HSD test. Values are means ± 1 standard errors during the entire year but not for SOC and TN.

It is noteworthy that the activities of animals, bivalve molluscs in particular, can also accelerate SOC decomposition in mariculture systems. Declines of quantity and quality of SOC have been documented in the no-feeding shellfish farms in a subtropical estuary (Ao River estuary, China)[35]. Bioturbation and bioirrigation associated with the burrowing, feeding, and other activities of molluscs can mix, flush and suspend the

sediments, resulting in oxygenation of sediments and elevated accessibility of organic matters to microorganisms, which favors the sediment respiration and decomposition of SOC (ref. [36]).

## 2.2 Impacts on $CH_4$ fluxes

Significant differences were also observed in the magnitude and seasonal pattern of $CH_4$ fluxes between *S. alterniflora* marsh and mariculture ponds (Fig. 1c). In the saltmarsh, daily $CH_4$ fluxes gradually increased from the start of the growth season in April, peaked on August, and then decreased to near zero during the wintertime. In the ponds, $CH_4$ fluxes were low at the beginning of the culturing period, then steadily increased and reached the first peak in July-August. From mid-August, $CH_4$ fluxes declined and were maintained low until draining. Drainage triggered the second peaks of $CH_4$ emission and the highest $CH_4$ flux was measured in MP1 (Fig. 1d). Annual $CH_4$ emission in the *S. alterniflora* marsh was 144 kg $CH_4$ $ha^{-1}$, 83.8% of which occurred in growth season. Converting saltmarsh to mariculture ponds dramatically decreased $CH_4$ emission by 80.3–96.0%, with annual $CH_4$ emission in the ponds ranging from 5.77 to 28.3 kg $CH_4$ $ha^{-1}$. Similar to NEE, $CH_4$ emission exhibited a decreasing trend with culturing time, which was 3.91 times greater in MP1 than in MP3 (Fig. 2b). $CH_4$ emission during culturing period in the ponds was 3.93–19.2 kg $CH_4$ $ha^{-1}$, contributing 62.2–68.1% annual budget. While $CH_4$ emission in drainage period mainly occurred in the initial 10 days, contributing more than half of the emission (Figs. 1c and 2b).

Poffenbarger et al.[37] proposed a salinity threshold of > 18 ppt for coastal wetlands that $CH_4$ emission could be neglected, which has recently been adopted by IPCC (ref. [20]). However, our results suggested that vegetated coastal saltmarsh could still emit appreciable $CH_4$ albeit the high salinity (28.4 ppt). In a previous study, we found that 67.3% of $CH_4$ produced in *S. alterniflora* marsh originated from 'noncompetitive' trimethylamine[38], as methanogens are often outcompeted for acetate or $H_2$ by sulfate reduction in marine environments. These methylamines can be produced during the decomposition of the cytoplasmic osmolytes (e.g., glycine betaine, choline, and proline) of marine plants[39], supporting substantial $CH_4$ production in *S. alterniflora* marsh. We had expected that converting *S. alterniflora* marsh to mariculture ponds would increase $CH_4$ emission, as anthropogenic labile organic C inputs and continuous inundation may favor $CH_4$ production in the ponds. In contrast to our expectations, this conversion significantly reduced $CH_4$ emission (Fig. 2b), which could be related to the decreased total C inputs and substrate availability. In *S. alterniflora* marsh, annual gross C assimilation was 17.8 Mg C $ha^{-1}$, which was 18 times higher than the C inputs from feeds and fertilizers in mariculture ponds (0.73 Mg C $ha^{-1}$, Supplementary Table 1). Here, C inputs from primary production of phytoplankton and periphyton in the ponds were not quantified. However, previous study reported an annual net autotrophic C fixation of 182–218 g C $m^{-1}$ in an analogous crab-shrimp-clam polyculture system adjacent to our sites[40]. Therefore, we consider that when primary productivity in the ponds was counted, C inputs for mariculture ponds were still much lower than that in *S. alterniflora* saltmarsh, which eventually decreased the supply of methanogenic substrates. We have speculated that, compared with plant residues, organic compounds in the feeds (e.g., starch and protein) can be more easily decomposed and become as substrates, especially "noncompetitive" methylamines[17,23]. Indeed, $CH_4$ emission factor of applied/inputted C ($EF_C$) in test ponds (1.43%) was 2.35 times that in *S. alterniflora* marsh (0.61%), indicating that the inputted C could be more

efficiently converted to $CH_4$ in mariculture ponds. However, the considerably lower $CH_4$ emissions in the mariculture ponds suggested that the benefit of higher C decomposability was completely offset by the loss of primary production.

More important, conversion of *S. alterniflora* saltmarsh to mariculture ponds significantly reduced SOC by 14.6–29.7%, and especially DOC by 65.2–74.1% (Table 1). Although the importance of recent photosynthates as source of $CH_4$ has been widely reported, SOC still accounted for a large fraction of $CH_4$ production in wetlands[41,42]. For example, 40–96% of emitted $CH_4$ from paddy fields originated from SOC (ref. [42,43]). Consistently, Kankaala and Bergström[44] found that the SOC-derived $CH_4$ contributed more than 90% to the total $CH_4$ emission from a shallow boreal lake. Particularly, $CH_4$ emission, SOC and DOC concentration in the ponds decreased with culturing age, and MP1 had the higher $CH_4$ emission and organic C contents relative to MP2 and MP3. Hence, SOC decomposition partly, at least, supported $CH_4$ production, since the application rates of feed and fertilizer were identical. Alongside with decreased substrate availability, changes in hydrological condition may also contribute to the reduction of $CH_4$ emission. Compared with the intermittently flooded saltmarsh, the ponds were permanently inundated during the culturing period (Supplementary Fig. 2). Generally, permanent inundation can create ideal anaerobic condition favoring $CH_4$ production[45]. However, the standing water can also act as a diffusion barrier which may suppress $CH_4$ emission by increasing $CH_4$ oxidation during transport[46]. Here, the maximal $CH_4$ fluxes in the ponds were observed in the early drainage period (Fig. 2d). Given the low temperature of this stage (early winter) and aerobic/semi-anaerobic condition, we consider that the emitted $CH_4$ was not currently produced but was a release of trapped $CH_4$ produced in culturing period. Inevitably, prolonged transport process increased the chance of $CH_4$ being oxidized. Nykänen et al.[47] found that up to 97.5% of $CH_4$ produced in a shallow small lake was oxidized before reaching the atmosphere. In contrast, $CH_4$ transport could proceed quickly in saltmarsh via aerenchyma tissue of *S. alterniflora*, which may also help bypass oxidation in soil zones[48].

## 2.3 Impacts on $N_2O$ fluxes

In *S. alterniflora* saltmarsh, $N_2O$ fluxes were at a low level and fluctuated within a narrow range between weak uptakes (−24.1 μg $N_2O$ $m^{-2}$ $h^{-1}$) and emissions (27.7 μg $N_2O$ $m^{-2}$ $h^{-1}$), while uptake frequently occurred in summer and autumn (Fig. 1e). In mariculture ponds, basal manure application and the first supplemental fertilizing did not stimulate $N_2O$ fluxes. After the second supplemental fertilizing, a peak of $N_2O$ flux was observed, albeit the relatively lower rates. Similar to $CH_4$ fluxes, a burst of $N_2O$ was observed immediately upon drainage (Fig. 1f). Annually, *S. alterniflora* marsh was a weak sink of atmospheric $N_2O$ (−0.04 kg $N_2O$ $ha^{-1}$) and 68.3% of the $N_2O$ uptakes occurred in growth season (Fig. 2c). However, converting saltmarsh to mariculture ponds produced a shift to $N_2O$ source. Annual $N_2O$ emission in the ponds ranged from 1.06 to 1.11 kg $N_2O$ $ha^{-1}$. In spite of the shorter time and lower temperature, drainage period $N_2O$ emission was higher than that in culturing period. Particularly, the initial 10 days of drainage period contributed 22.1–31.4% annual $N_2O$ budget (Fig. 2c).

Our annual $N_2O$ budget in the *S. alterniflora* marsh was comparable to the reported atmospheric $N_2O$ consumptions of 0.01–0.14 kg $N_2O$ $ha^{-1}$ $yr^{-1}$ in coastal saltmarshes which receive limited anthropogenic N loading[49,50]. These data supported the view of productive and pristine saltmarshes as negligible sources or even small sinks of atmospheric $N_2O$ (ref. [49]). However, converting *S. alterniflora* marsh to mariculture ponds fundamentally shifted the $N_2O$ sink to a net source of $N_2O$. At least two explanations can be proposed. First, soil mineral N for nitrifiers and denitrifiers was considerably increased following the conversion (Table 1). Generally, N is the key limiting nutrient in pristine coastal wetlands. Here annual mean $NO_3^-$ in the *S. alterniflora* marsh was only 0.14 mg N $kg^{-1}$, a value that was lower than the threshold (5 mg N $kg^{-1}$) for denitrification[51] and was close to the threshold (~ 1 mg N $kg^{-1}$) for denitrifiers using $N_2O$ as the unique electron acceptor[52]. Hence, the lack of $NO_3^-$ might be responsible for negative $N_2O$ fluxes in *S. alterniflora* marsh. Conversely, mineral N concentrations in the ponds were a magnitude higher (Table 1). The mariculture ponds received higher N inputs from feeds and fertilizers while only a small part of the added N (~ 25%) was converted to fish biomass, leading to large amount of residual active N accumulated and facilitating $N_2O$ production in the ponds[16,17]. Second, Chen et al.[53] found that $N_2O$ production via denitrification relies on $NO_3^-$/DOC ratio in soils. The relatively lower DOC concentration and higher $NO_3^-$/DOC ratio in ponds could increase the proportion of $N_2O$ in denitrification products since high DOC content increases electron pressure, facilitating $N_2O$ reduction and resulted in a lower ratio of $N_2O/(N_2O + N_2)$ or even net $N_2O$ consumption, especially in anaerobic environments[54]. Senbayram et al.[55] pointed out that when soil $NO_3^-$ concentrations fell below 20 mg $kg^{-1}$, organic substrate addition would sharply reduce $N_2O$ emission in anaerobic soils. In aquaculture systems, the lack of organic electron donors for $N_2O$ reduction was also recognized as a major reason for $N_2O$ emissions[56], whereas carbohydrate (starch) addition was noted to dramatically reduce $N_2O$ emission by 83.4% in an intensive tilapia culturing system[57]. Therefore, it is likely that the elevated $NO_3^-$ and lowered DOC availability collectively increased $N_2O$ emission via denitrification following the conversion of saltmarsh to mariculture ponds.

As well as with the change in magnitude, $N_2O$ fluxes in mariculture ponds showed distinct temporal patterns from that in *S. alterniflora* marsh. Substantial $N_2O$ fluxes were triggered by pond draining. This finding agreed well with previous studies that observed drainage episodes as the critical period for $N_2O$ emission from aquaculture ponds[21,22,58]. As discussed above, abundant soil $NO_3^-$ usually generates a higher ratio of $N_2O/(N_2 + N_2O)$ because $NO_3^-$ is preferred over $N_2O$ as an electron acceptor[59]. The ratio also increases if some oxygen ($O_2$) is present, because the inhibition of $N_2O$ reductase by $O_2$ is stronger than the other reductases involved in denitrification[60]. On the other hand, the draining pond soil was still saturated initially and might cause optimum moisture condition (~ 80% water-filled pore space in soil) for a large proportion of $N_2O$ produced during denitrification[58,59]. Furthermore, with no standing water, $N_2O$ could diffuse more easily and escape from consumption compared to the waterlogging condition. Hence, we consider these factors have collectively contributed to the $N_2O$ emission pulse in the early stage of the drainage period.

## 2.4 Full GHG debt of mariculture ponds

Although aquaculture is often inferred as important sources of GHG to the atmosphere[61,62], only a few studies could comprehensively account for the GHG emissions associating with the conversion of natural coastal wetlands. Here, we incorporated the direct fluxes of $CO_2$, $CH_4$, and $N_2O$ to evaluate their net global warming potential (nGWP) of each system. Annually, mariculture ponds exerted an overall positive net radiative forcing impact of 2.16 Mg $CO_2$eq $ha^{-1}$ over a 100-year time horizon, with $CO_2$, $CH_4$, and $N_2O$ accounting for 68.9%, 18.0%, and 13.2% of the nGWP, respectively (Fig. 2d). Among the ponds, MP1 held up the highest nGWP (3.22 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$), primarily due to its higher NEE and $CH_4$ emissions relative to the older ponds. In contrast to mariculture ponds, *S. alterniflora* marsh showed a negative nGWP of −13.8 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$. This substantial negative value was mainly attributed to the high $CO_2$ uptake by plants, despite 22.6% of its climatic cooling impact was offset by the simultaneous $CH_4$ emission. Specifically, the negative nGWP of *S. alterniflora* marsh indicated that its conversion to mariculture ponds caused the loss of foregone GHG mitigation capacity by the saltmarsh[63], yielding a full GHG debt of 15.9 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$. This value was 7.36-fold higher than their direct GHG emissions from the mariculture ponds.

## 2.5 Comparison with other animal protein production sectors

We compared the direct GHG emissions from our mariculture ponds with those from other aquaculture systems in China, e.g., freshwater crab ponds (< 0.5 ppt) and brackish shrimp ponds (4.2 ppt) (ref. [17,26,64]). We found that, in spite of the differences in C and N inputs and operation scenarios, nGWP and yield-scaled GWP (GHGI) in aquaculture systems decreased significantly along the gradient of salinity (Fig. 3a,b). Our estimates of nGWP and GHGI in the polyhaline mariculture ponds (28.4 ppt) were just 8.51–13.7% and 1.38–14.9% of those in freshwater and brackish ponds. This difference was mainly attributed to the minor $CH_4$ emission in our ponds, given $N_2O$ and $CO_2$ emissions were much comparable among three systems. Salinity can strongly impact $CH_4$ production by regulating the availability of sulfate. In contrast to polyhaline water ponds where $CH_4$ production was inhibited by presence of sulfate, lower salinity and sulfate availability in freshwater and brackish aquaculture ponds allowed intense $CH_4$ production from $H_2/CO_2$ and acetate, whereas these “competitive” substrates can be easily decomposed from residues of feeds and submerged macrophytes[17,23]. This result substantiates the role of $CH_4$ emission in GHG budgets of aquaculture systems and suggests that mariculture at high salinity could have substantial lower direct GHG-cost relative to freshwater and brackish aquaculture due to their virtual low $CH_4$ emissions.

We also compared the full GHG debt in aquaculture systems with the estimates from other animal protein production sectors on a kg $CO_2$eq $kg^{-1}$ protein basis (GHGI-protein) (Fig. 3c). Similar to nGWP and GHGI, the direct GHGI-protein in our mariculture ponds (6.48 kg $CO_2$eq $kg^{-1}$ protein) was significantly lower than that in freshwater crab (185 kg $CO_2$eq $kg^{-1}$ protein) and brackish shrimp (14.7 kg $CO_2$eq $kg^{-1}$ protein) ponds, but was higher than that in a no-feeding oyster farm (0.13 kg $CO_2$eq $kg^{-1}$ protein) (ref. [65]). Notably, we found the GHGI-protein in aquaculture systems were much lower than those from terrestrial livestock production (39.5–466 kg $CO_2$eq $kg^{-1}$ protein), except for freshwater crab ponds. However, when the loss of foregone GHG mitigation capacity of pristine wetlands was counted, GHGI-protein in our mariculture ponds would increase to 46.7 $CO_2$eq $kg^{-1}$ protein, which is higher than poultry but still lower than beef, small ruminants, or pork production. These results imply that mariculture can provide a low-GHG animal protein source relative to freshwater

aquaculture and livestock production. Developing approaches to attenuate net emissions associated with the foregone GHG mitigation loss will be crucial for minimizing the climate impact of mariculture. Future aquaculture programs could preferentially engineer aquaculture systems by conversion of lowly productive sites (e.g., saline bare land, abandoned ponds, etc.) and carrying out it in high-salinity waters[30,31], as reduced foregone C sequestration losses and $CH_4$ emissions could be simultaneously achieved under such conditions.

Overall, our results show that the conversion of saltmarsh to mariculture ponds in coastal region of China creates a GHG debt of 15.9 Mg $CO_2$eq $ha^{-1}$ $yr^{-1}$. Within them, the loss of foregone GHG mitigation capacity of pristine wetlands makes the largest contributions (86.4%) to overall GHG debt, whereas the other 15.6% arises from the direct emission of $CO_2$, $CH_4$, and $N_2O$ in the mariculture ponds. This finding contributes to growing recognition of the climatic roles of mariculture and highlights the importance of taking the foregone C sequestration losses associated with coast wetlands conversion into the full GHG accounting. Nonetheless, the GHG-cost of protein in mariculture was much lower than inland freshwater aquaculture and the major terrestrial livestock productions (such as beef, small ruminants, and pork), indicating mariculture can provide a low-GHG animal protein source. For initiatives aiming at reduction of GHG emissions, future aquaculture should primarily avoid conversion of the highly productive coastal wetlands, and further minimize $CH_4$ emissions by using high-salinity waters.

# 3. Methods

## 3.1. Site locations

The study site is located at the coast of Yellow Sea, Yancheng City, Jiangsu Province, China (33°23'N, 120°43'E). This region is characterized by a subtropical monsoon climate with the long-term (1981–2010) mean annual air temperature of 14.3°C and precipitation of 1067 mm. Tides in this region are typically semidiurnal with amplitude of 2–3 m and tidewater salinity of 30.0–32.0‰. Native plant *Suaeda salsa* used to be the dominant species in this site until *S. alterniflora* was intentionally introduced in 1982. Since then, exotic *S. alterniflora* gradually replaced the native plants and established monoculture communities in the intertidal zone[66]. Expansion of aquaculture in this region initiated in early 1980s and represented the primary causes of coastal wetlands loss in recent years. During 2000–2017, Yancheng City lost 608 $km^2$ natural coastal wetlands and more than 35% of them were converted to aquaculture ponds[67].

## 3.2. Experimental design and field measurement

Field experiments were carried out throughout April 2016 to May 2017 in a *S. alterniflora* marsh and three adjacent saltmarsh-converted mariculture ponds (Supplementary Fig. 1). These ponds were converted from the *S. alterniflora* marsh in 2010, 2011, and 2014, respectively, which represented a conversion chronosequence of 1- (MP1), 4- (MP2), and 5-year (MP3) at beginning of the experiment. Generally, aquaculture period in this region usually starts in April and ends in November. In line with the local aquaculture practices, we adopted the similar aquaculture mode and operating scenario in the experimental ponds. Briefly, common prawn (*Mercenaria mercenaria*)-crab (*Portunus trituberculatus*)-clam (*Exopalaemon carinicauda*) polyculture was employed in these ponds. Crabs and prawn were fed with commercial feed pellets and trash fish until they were harvested, and fertilizers were also applied to stimulate phytoplankton and clam production (Supplementary

Tables 1 and 2). Annually, total inputs of C and N were 725 kg C $ha^{-1}$ and 268 kg N $ha^{-1}$, respectively. The water regime was also in line with local practice. Prior to clams stocking, sea water was introduced into ponds from an adjacent tidal creek. In the end of the culturing period, these ponds were drained to facilitate harvesting. Crab and prawn were harvested in late September, followed by clam harvesting. Detailed management practices in these mariculture ponds are shown in Supplementary Table 2 and elaborated in Supplementary Text 1 (Methods-Extensive).

## 3.3. Measurement of greenhouse gas fluxes

Eddy covariance (EC) method was used to quantify the ecosystem-scale $CH_4$ and $CO_2$ (net ecosystem $CO_2$ exchange, NEE) fluxes from *S. alterniflora* marsh. $CO_2$ and $CH_4$ fluxes were computed as the covariance between fluctuations in gas mixing ratio and vertical wind velocity over 30 min periods. We gap-filled the missing NEE using the marginal distribution sampling algorithm and further partitioned it into gross primary productivity (GPP) and ecosystem respiration (Re). GPP and Re were all presented with positive signs (NEE = Re – GPP). For $CH_4$ fluxes, we used the random forest (RF) to fill the data gaps with meteorological variables. Details regarding the EC flux and ancillary measurements, data processing, gap filling are elaborated in Supplementary Text 1. As EC $N_2O$ flux measurements are limited by the detection accuracy of the instrumentation, especially for natural ecosystems where $N_2O$ fluxes are generally weak[68], here we measured $N_2O$ flux in *S. alterniflora marsh* using the static closed chamber technique. Four gas sampling plots were randomly established in *S. alterniflora marsh* ~ 20 m away from the EC tower, and $N_2O$ flux was measured using the transparent Plexiglass chambers.

The static closed chamber method was also used to measure $CO_2$, $CH_4$ and $N_2O$ fluxes in mariculture ponds. Four subsites were randomly selected in each pond to minimize the spatial uncertainties of GHG emissions. GHG fluxes were also measured by the transparent chambers, and thus the measured $CO_2$ fluxes in mariculture ponds were recognized as NEE (ref. [50]). The chamber deployment, sampling procedures and configuration of the GC for measuring GHG fluxes are extensively included in Supplementary Text 1.

## 3.4. Annual GHG budgets and radioactive forcing calculation

Annual $CO_2$ and $CH_4$ budgets in *S. alterniflora* marsh were calculated by integrating the gap-filled and partitioned fluxes over the course of a full year. For $N_2O$ emission in *S. alterniflora* saltmarsh and $CO_2$, $CH_4$, and $N_2O$ emissions in mariculture ponds, the annual budgets were calculated by linear interpolation between measuring days. The net radiative forcing arising from annual $CO_2$ (NEE), $CH_4$, and $N_2O$ budgets was calculated using the net global warming potential (nGWP, kg $CO_2$eq $ha^{-1}$ $year^{-1}$) methodology[69]:

$$nGWP = 28 \times CH_4 + 265 \times N_2O + 1 \times CO_2$$

where $CH_4$, $N_2O$ and $CO_2$ denote annual emissions of $CH_4$ (kg $CH_4$ $ha^{-1}$), $N_2O$ (kg $N_2O$ $ha^{-1}$) and NEE (kg $CO_2$ $ha^{-1}$), respectively.

Thereafter, the greenhouse gas intensity (GHGI, kg $CO_2$eq $kg^{-1}$ yield) and protein-based GHGI (GHGI-protein, kg $CO_2$eq $kg^{-1}$ protein) in mariculture ponds was calculated by dividing nGWP by yield biomass or protein[17].

Besides, the $CH_4$ emission factor of applied C ($EF_C$) and $N_2O$ emission factor of applied N ($EF_N$) in the ponds was calculated by dividing annual $CH_4$ or $N_2O$ emissions by total C or N inputs, respectively.

## 3.5. Environmental data

Micrometeorological instrumentation was deployed in the *S. alterniflora* saltmarsh to accompany EC measurements. Air temperature, precipitation, soil temperature at 10 cm depth, and water depth were synchronously measured. Salinity of the tide water was measured in a tidal creek about 60 m southeast of the tower. In mariculture ponds, water depth, water temperature (or soil temperature in drainage period), salinity, and dissolved $O_2$ of the pond water were measured simultaneously with gas sampling.

The 0–10 cm soil samples were collected weekly from the saltmarsh and mariculture ponds for mineral N and DOC measuring. SOC and total N (TN) contents were determined by the wet-oxidation method and the Kjeldahl procedure, respectively. The procedures for auxiliary measurements were also detailed in Supplementary Text 1.

## 3.6. Statistical analysis

Statistical analyses were performed using R version 3.2.2 unless otherwise stated. Data normality was examined using the Kolmogorov-Smirnov test, and natural-log transformation was used if necessary. One-way analysis of variance (ANOVA) with a Tukey's HSD test was used for comparison of soil properties cross sites and annual GHG emissions among ponds.

## Declarations

# Data availability

All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Source data for all $CO_2$, $CH_4$, and $N_2O$ fluxes and environmental data are provided with this paper.

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# Figures

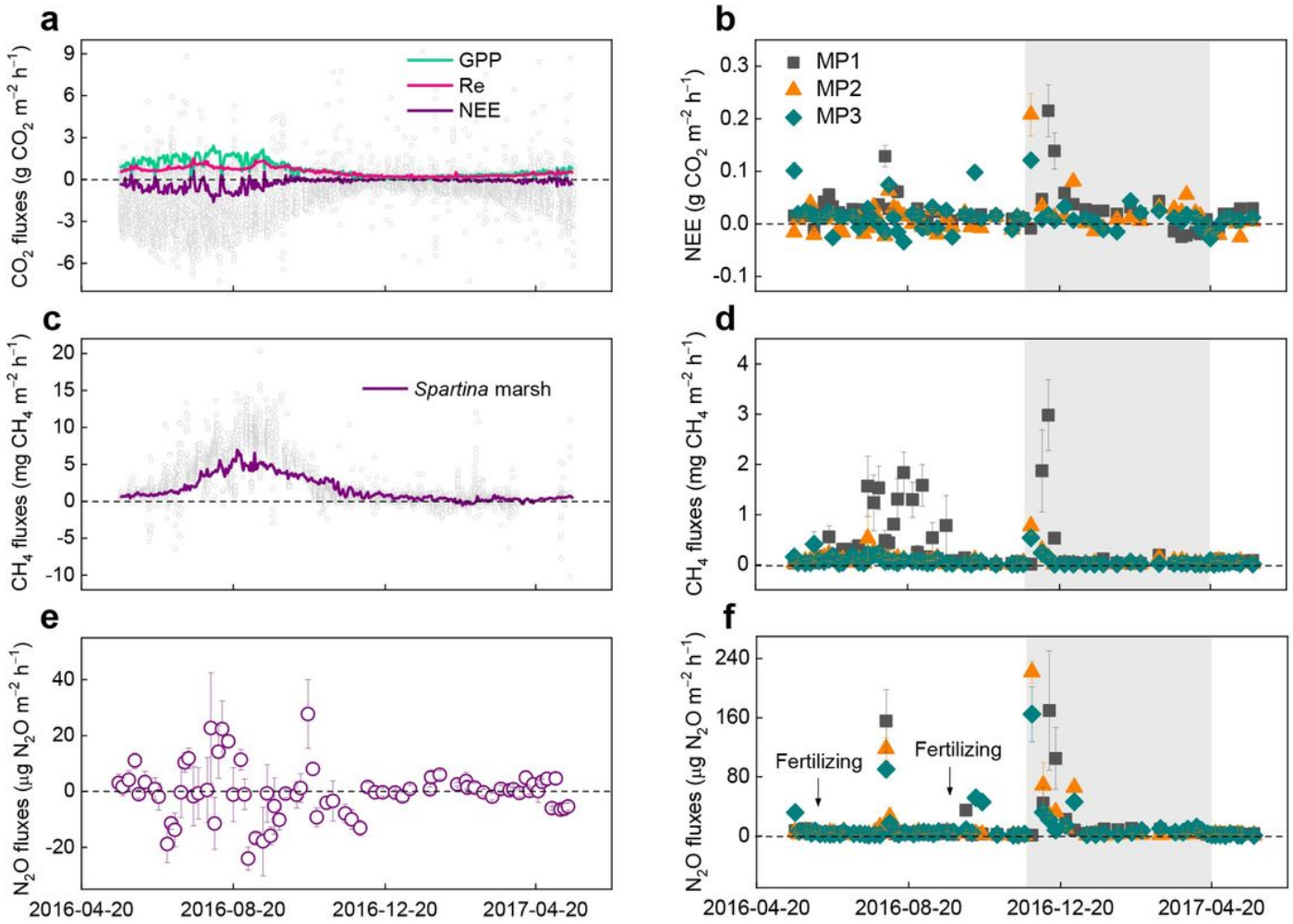


Figure 1

**Temporal variation of greenhouse gas fluxes in *S. alterniflora* saltmarsh and mariculture ponds.** Half-hourly (gray points) and daily gap-filled (purple lines) $CO_2$ (**a**) and $CH_4$ (**c**) fluxes in *S. alterniflora* saltmarsh were measured using the eddy covariance method. $N_2O$ flux in saltmarsh (**e**) and net ecosystem $CO_2$ exchange (NEE, **b**), $CH_4$ (**d**) and $N_2O$ (**f**) fluxes in mariculture ponds were measured by transparent Plexiglass chambers ($n$ = 4). Three mariculture ponds were converted from the *S. alterniflora* with a conversion chronosequence of 1- (MP1), 4- (MP2), and 5-year (MP3) at beginning of the experiment. Arrows denote the time of applying synthetic fertilizer and light gray shaded areas represent the drainage period for MPs.

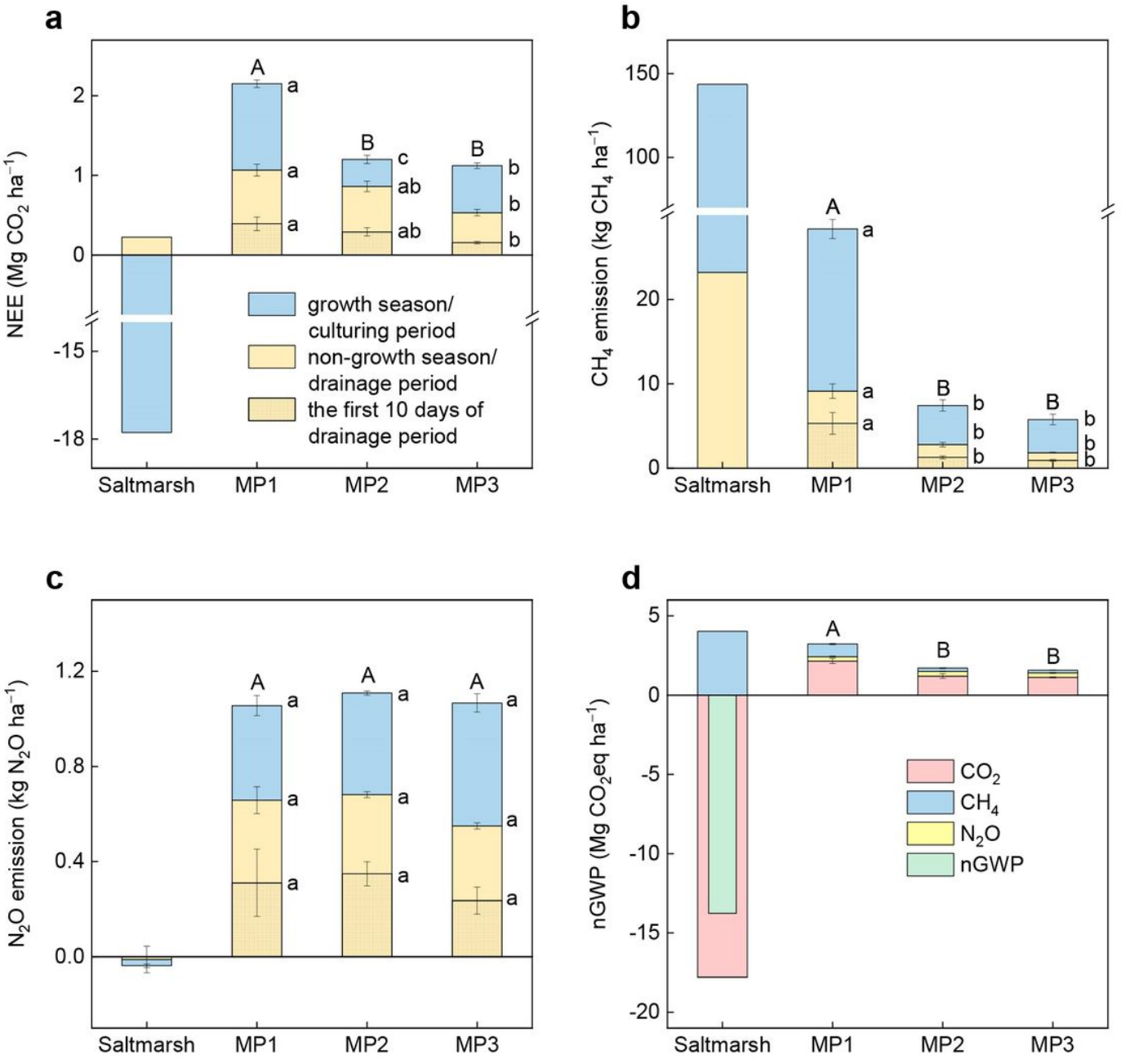



Figure 2

**Annual greenhouse gas emissions from the *S. alterniflora* saltmarsh and mariculture ponds during. a–c**, $CH_4$ (**a**), $N_2O$ (**b**) and $CO_2$ emissions (**c**) from the *S. alterniflora* saltmarsh and three mariculture ponds (MP1–3). Net global warming potential (nGWP, **d**) represents the radiative forcing arising from $CO_2$, $CH_4$, and $N_2O$ emissions according to IPCC methodology, e.g., nGWP = 28 × $CH_4$ + 265 × $N_2O$ + 1 × $CO_2$. Vertical bars are the standard errors of the means ($n$ = 4). Different capital letters denote significant differences between sites during the entire year and different lowercase letters denote significant differences between three ponds during the culturing period or drainage period ($P$ < 0.05, ANOVA, Tukey's HSD test).

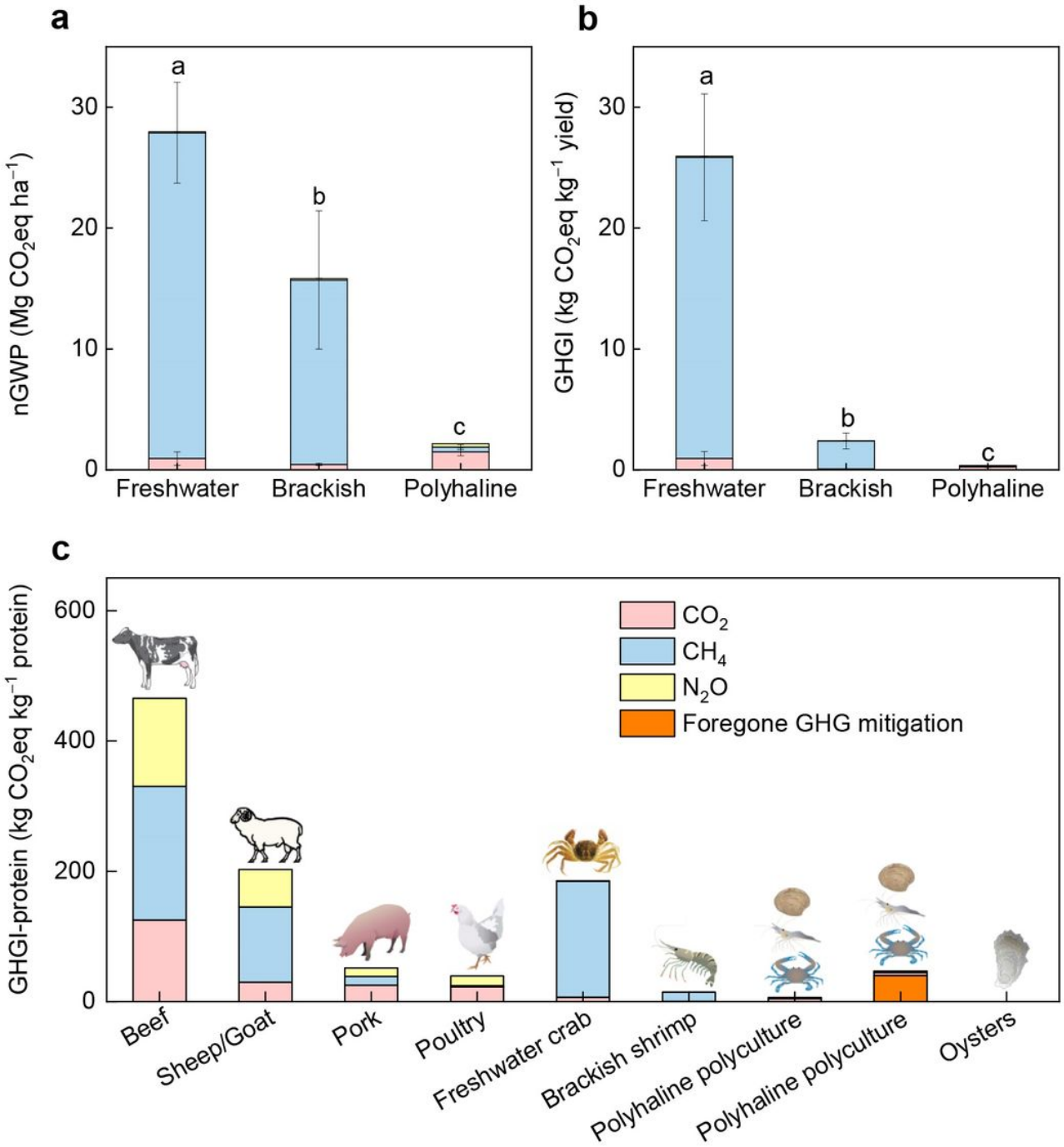



**Figure 3**

**Comparison of greenhouse emission from aquaculture and meat production. a—c**, estimated net global warming potential (nGWP, **a**), greenhouse gas intensity (GHGI, **b**) and protein-based GHGI (GHGI-protein, **c**) in aquaculture systems and terrestrial livestock production sectors. Different lowercase letters denote significant differences between aquaculture systems. Values of polyhaline mariculture were quantified in this study; values from freshwater, brackish, and no-feeding oyster aquaculture are from Yuan et al.[27], Yang et al.[26,64] and Ray et al.[65]; values from terrestrial livestock protein production are from Ray et al.[65] and references therein.

## Supplementary Files

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