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Submerged Macrophytes Enhance and Differentially Regulate Greenhouse Gas Emissions in *Eriocheir sinensis* Aquaculture Systems

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Abstract

Submerged macrophytes play a vital role in regulating carbon and nitrogen cycling in aquatic ecosystems; however, their effects on greenhouse gas (GHG) emissions in aquaculture systems remain poorly understood. This study quantified methane (CH_4) and nitrous oxide (N_2O) fluxes after planting *Hydrilla verticillata* (HV), *Elodea nuttallii* (EN), and *Vallisneria natans* (VN) in *Eriocheir sinensis* tanks to elucidate emission dynamics and identify low carbon management strategies. Compared with unvegetated controls, vegetated treatments significantly enhanced CH_4 emissions, with CH_4 contributing over 97% of the global warming potential (GWP). The overall GWP values were in the order HV > VN > EN > CK (control), indicating that *V. natans* had the lowest GWP value among all macrophyte treatments. Mechanistically, nitrogen availability and redox conditions jointly regulated GHG fluxes, while differences in aerenchyma development, root exudation, and algal attachment explained the observed species-specific variation. These findings suggest that optimizing plant composition, particularly through the introduction of *V. natans* or species with similar ecological traits, can effectively mitigate GHG emissions in crab aquaculture. Moreover, the identified mechanisms provide new insights into methane regulation in vegetated wetlands, supporting broader decarbonization strategies for aquatic ecosystems.

Keywords: submerged macrophytes; *Eriocheir sinensis*; greenhouse gas; global warming potential; aquaculture

1. Introduction

Global warming, primarily driven by increasing concentrations of greenhouse gases (GHG), poses an urgent environmental challenge. While carbon dioxide (CO_2) dominates anthropogenic emissions, methane (CH_4) and nitrous oxide (N_2O) exert disproportionately large climate forcing effects on centennial timescales (GWP_{100} ≈ 28 for CH_4 and ≈ 265 for N_2O), thus requiring targeted quantification of their emission sources [1]. Recent syntheses have shown that inland and coastal aquatic systems are important and spatially heterogeneous contributors to the global CH_4 and N_2O budgets [2–5]. These findings highlight the importance of conducting system-specific investigations to explore the mechanisms of GHG production and flux control in aquatic environments [6,7].

Submerged macrophytes exert various mechanisms to control the dynamics of aquatic GHG. Oxygen released from their roots and photosynthetic can elevate the redox potential of sediments, inhibiting anaerobic methanogenesis and promoting aerobic CH_4 oxidation [8]. Conversely, macrophytes also supply readily decomposable organic carbon, providing energy for

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methanogenesis and heterotrophic respiration [9]. Their aerenchymatous tissues facilitate plant-mediated CH_4 transport from sediments to the atmosphere, effectively bypassing oxidative layers [10]. Regarding the nitrogen cycling, alterations to the nitrification-denitrification pathways caused by macrophytes can either enhance complete denitrification to produce N_2 or promote the accumulation of N_2O, depending on nitrate availability and the redox microgradients. Therefore, empirical studies report contrasting effects of submerged plants; some species enhance CH_4 release, while others suppress it, indicating a strong species- and environment-dependent effect [11,12].

Aquaculture ponds differ fundamentally from natural water bodies in the factors influencing GHG generation and emission pathways [13]. Intensive feeding and stocking increase the input of organic matter and nitrogen [14,15], while water exchange and sediment disturbance during management modify oxygen dynamics and substrate availability [16]. Bioturbation by cultured organisms further redistributes nutrients and organic carbon in sediments, altering redox gradients critical for methanogenesis and denitrification. Therefore, mechanistic patterns derived from lakes or wetlands cannot be directly applied to aquaculture systems, which have been identified as concentrated hotspots for CH_4 and N_2O emissions in regional inventories [16]. In freshwater aquaculture in China, submerged macrophytes such as *Hydrilla verticillata* (HV), *Vallisneria natans* (VN), and *Elodea nuttallii* (EN) are typically introduced into *Eriocheir sinensis* ponds to stabilize water quality and improve habitat structure. However, the effects of these plants on GHG emissions remain uncertain. While root oxygenation and enhanced redox conditions may inhibit methanogenesis and N_2O formation [8], labile carbon release and plant-mediated gas transport may counteract these benefits [10]. Recent studies have shown that plant-specific traits, such as aerenchyma structure, root exudation, and epiphytic algal colonization, significantly influence CH_4 and N_2O fluxes [17]. Given the prevalence of strong anthropogenic influences and nutrient enrichment in aquaculture ponds, elucidating the interactions between these plant and GHG is essential for developing low-carbon management strategies.

Therefore, this study aimed to investigate the effects of different submerged macrophytes (*H. verticillata*, *V. natans*, and *E. nuttallii*) on CH_4 and N_2O emissions in an *E. sinensis* aquaculture system. Specifically, the objectives were: to (i) quantify the CH_4 and N_2O fluxes under different macrophyte treatments and an unvegetated control, (ii) to identify key water quality parameters influencing GHG emissions, and (iii) to assess the overall contribution of submerged plants to GHG emissions. The results provide new insights into the mechanisms of GHG release in aquaculture ecosystems and highlight that macrophyte coverage often enhances the total GHG emissions in *E. sinensis* culture tanks.

2. Materials and Methods

2.1. Site Description

The study was conducted in the Datong Lake District of Yiyang City, Hunan Province, China (29°01′19″ N, 112°15′28″ E). The region has a humid continental monsoon climate, transitioning from the central to the northern subtropical zone. The mean annual temperature is 16.5 °C, and the water temperature typically ranges from 10 °C to 34 °C throughout the year. In the surface soil at the experimental site, the total nitrogen content was 1.34 $g \cdot kg^{-1}$, the total phosphorus content was 0.70 $g \cdot kg^{-1}$ and the total carbon content was 24.12 $g \cdot kg^{-1}$.

2.2. Experimental Design and Management

This experiment, conducted from 23 July to 23 August 2024, aimed to investigate the effects of different submerged macro phytes on CH_4 and N_2O emissions in *Eriocheir sinensis* aquaculture systems. Four treatments were established: *H. verticillata* (HV), *V. natans* (VN), *E. nuttallii* (EN), and a plant-free control (CK), with three replicates per treatment. Cylindrical polyethylene tanks (height: 1.0 m; radius: 0.7 m) were buried underground to simulate a pond environment, containing 0.2 m of bottom sediment and 0.75 m of overlying water.

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During the 30-day experiment, CH_4 and N_2O fluxes were measured every five days between 08:30 AM and 11:00 AM, for a total of six samplings. Prior to stocking, submerged macrophytes were acclimated for one week. Juvenile *E. sinensis* were then introduced at a density of 1.3 plants·m^{-2}. During the culture period, *E. sinensis* were fed commercial pelleted diet daily at 6:00 PM, with a crude protein content of not less than 36%. All treatments employed the same feeding schedules and water management practices to ensure consistency of experimental conditions.

2.3. Sampling and Analysis

CH_4 and N_2O fluxes were measured using static dark chamber gas chromatography (GC). The dark chamber was constructed of an opaque PVC cylinder (height: 0.5 m; diameter: 0.4 m) and equipped with an external insulation layer to minimize temperature fluctuations. Each chamber was equipped with a gas sampling port and a thermometer, with the sampling port connected to a three-way valve and a syringe via a flexible hose (Figure 1). During sampling, the chamber was fixed to stainless steel brackets and submerged in water for approximately 5 cm to ensure airtightness. Prior to sampling, chambers were equilibrated for 30 min. Gas samples were collected at 0, 15, 30, 45, and 60 min using a 30 mL syringe, injected into pre-evacuated glass vials, and stored in the dark until analysis. The internal temperature of the chamber was recorded simultaneously. Gas concentrations were determined using a gas chromatograph (8890, Agilent Technologies, China).

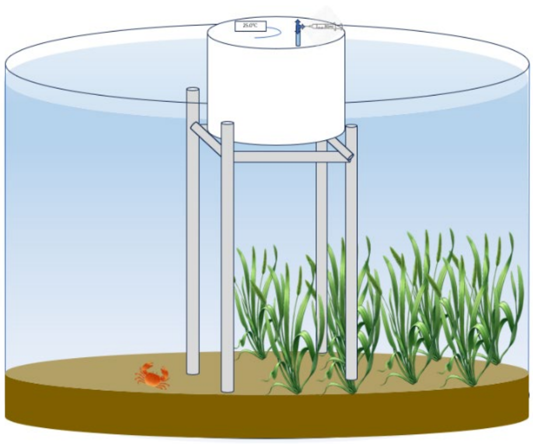

Figure 1. Schematic diagram of the layout of the experimental breeding tank and sampling box.

Simultaneously with gas sampling, 500 mL of mid-layer water was collected in a polyethylene bottle and immediately stored in the dark at - 4 °C. Nutrient and organic carbon contents were then analyzed. Total nitrogen (TN), total phosphorus (TP), and nitrate nitrogen (NO_3^-–N) were determined using an AA3 flow injection analyzer (Auto Analyzer 3-AA3, SEAL Analytical, USA). Total organic carbon (TOC) was measured using a total organic carbon analyzer (TOC-Vwp, Shimadzu, Japan). Dissolved oxygen (DO), water temperature (WT), the value of Eh, total dissolved solids (TDS), and chlorophyll (Chl) were measured in-situ using a multiparameter water quality analyzer (EXO, Xylem Analytics, China).

2.4. Flux Calculations

CH_4 and N_2O fluxes (*f*) were calculated as [18]:

$$f = \rho \times h \times P/P_0 \times \mathrm{dc/dt} \times 273/(273 + T) \quad (1)$$

where *f* is the flux of CH_4 or N_2O (mg·m^{-2}·h^{-1}), ρ is the gas density of CH_4 (0.717) or N_2O (1.977) (kg·m^{-3}), *h* is the height of the chamber above the water surface (m), *P* is the local atmospheric pressure (Pa), P_0 is the standard atmospheric pressure (Pa), *dc*/*dt* is the concentration change rate (mg·m^{-3}·h^{-1}), and *T* is the water temperature (°C).

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Cumulative emissions (*F*) were calculated as [18]:

$$F = \sum_{i=1}^{a} \left[\frac{f_{i+1} + f_i}{2} \times (t_{i+1} - t_i) \times 10^{-2} \times 24 \right] \quad (2)$$

where *F* is the cumulative emission (kg·ha^{-1}), *f* is the gas flux (mg·m^{-2}·h), ($t_{(i+1)} - t_i$) is sampling interval (days), 10^{-2} is the unit conversion factor, and 24 is the hourly conversion factor.

Global warming potential (GWP) was estimated on 100-year horizon as [19]：

$$GWP = F_{CH_4} \times 28 + F_{N_2O} \times 265 \quad (3)$$

where F_{CH4} and F_{N2O} are the cumulative emissions of CH_4 and N_2O (kg·ha^{-1}), respectively.

2.5. Data Processing and Statistical Analysis

All statistical analyses were performed using Microsoft Office 2019 and Origin 2024. Differences among treatments were evaluated using one-way analysis of variance (ANOVA), followed by Tukey's honest test to determine pairwise significance. Pearson product-moment correlation coefficient was used to assess the correlation between GHG fluxes and water quality factors. Statistical significance was defined as $p < 0.05$.

3. Results

3.1. Temporal Dynamics and Cumulative Fluxes of GHG Emissions

CH_4 fluxes exhibited a pronounced bimodal temporal pattern across all treatments. Emissions increased steadily during the initial 5 to 20 days, reaching the first peak around day 20, followed by a brief decline near day 25, most notably under the *E. nuttallii* (EN) treatment. Subsequently, CH_4 fluxes rose sharply again, reaching their maximum values at the end of the monitoring period (Figure 2a). Significant differences were observed among treatments ($p < 0.05$). Throughout the experiment, the *H. verticillata* (HV) group consistently exhibited the highest emission rate, with peak fluxes exceeding 70 mg·m^{-2}·h^{-1} and mean fluxes significantly higher than those of all other groups. The EN group followed, with a peak flux of approximately 65 mg·m^{-2}·h^{-1}, while the *V. natans* (VN) group showed moderate emissions, peaking at approximately 55 mg·m^{-2}·h^{-1}. In contrast, the CH_4 emissions from the CK treatment group were almost negligible, indicating that it had the strongest emission mitigation effect (Figure 2a). Cumulative CH_4 emissions displayed a clear gradient: HV > EN > VN > CK (Figure 2b). Significant differences in cumulative methane emissions were observed among the different treatment groups, all of which were significantly higher than those of CK ($p < 0.05$) (Figure 2b). The total emission from the HV treatment (250.10 ± 7.91 kg·hm^{-2}) was approximately 15 times higher than that of the CK treatment.

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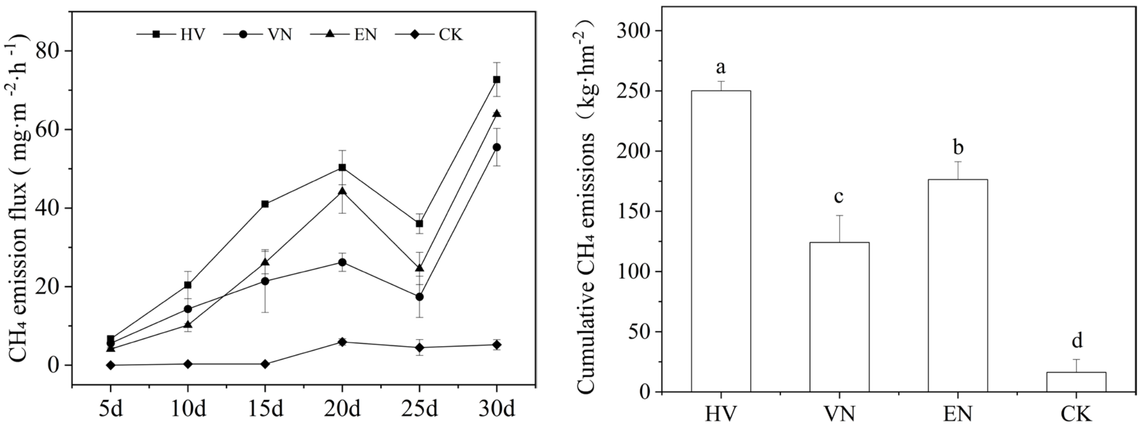
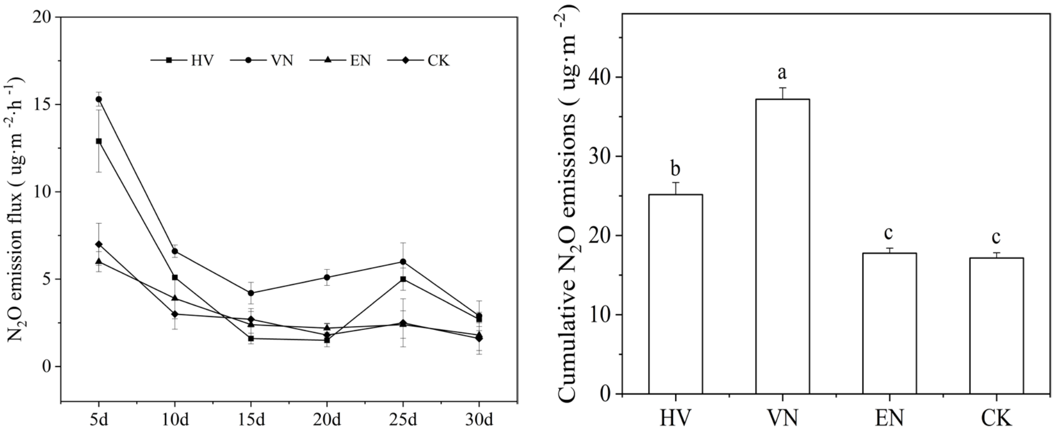


(a) (b)

Figure 2. Dynamic changes in CH_4 emission flux under different submerged macrophytes (a) and cumulative emissions during the experiment (b). The bars represent the standard error range, and the same lowercase letter above the bars indicates no statistically significant difference ($p > 0.05$). HV, group with *Hydrilla verticillata*; VN, group with *Vallisneria natans*; EN, group with *Elodea nuttallii*; CK, plant-free control.

In contrast, the trend of N_2O flux was opposite to that of CH_4. Emissions were concentrated in the early stages of the experiment, with overall emissions decreasing throughout the experiment, slightly rebounding around day 25, and then declining to the lowest level at the end of the monitoring period (Figure 3a). The VN group demonstrated the highest N_2O fluxes, with an early peak of approximately 15 $\mu g \cdot m^{-2} \cdot h^{-1}$ and the highest mean emission rate across all groups. The HV group ranked second, with an initial peak close to 13 $\mu g \cdot m^{-2} \cdot h^{-1}$, but then rapidly declining. Both the EN and CK groups maintained relatively low and stable fluxes, with an early peak of 7 $\mu g \cdot m^{-2} \cdot h^{-1}$, indicating strong N_2O mitigation potential (Figure 3a). The cumulative N_2O emissions followed the order VN > HV > EN ≈ CK (Figure 3b). The VN treatment yielded the highest cumulative emissions (37.2 ± 1.45 $\mu g \cdot m^{-2}$), 116.78% higher than that of the CK treatment, while the HV treatment exceeded the control by 46.69%. These results collectively indicate that submerged macrophytes, particularly *H. verticillata* and *V. natans*, significantly enhanced greenhouse gas emissions in *E. sinensis* aquaculture tanks, while the unvegetated control group showed the best emission mitigation effect on both CH_4 and N_2O fluxes.



(a) (b)

Figure 3. Dynamic changes in N_2O emission flux under different submerged macrophytes (a) and cumu lative emissions during the experiment (b). The bars represent the standard error range, and the same lowercase letter above the bar indicates no statistically significant difference ($p > 0.05$). HV, group with *Hydrilla verticillata*; VN, group with *Vallisneria natans*; EN, group with *Elodea nuttallii*; CK, plant-free control.

3.2. Global Warming Potential

All treatments emitted both CH_4 and N_2O, and there were significant differences in total GWP among the treatments ($p < 0.05$). The overall ranking was HV > EN > VN > CK (Figure 4). Compared with the unvegetated control group, the systems with submerged macrophytes had significantly higher GWP values ($p < 0.05$), with HV exhibiting the highest overall warming effect, approximately 13.8 times that of CK.

Although the warming effect of all vegetated treatments was significantly higher than that of the control group, significant differences were observed among different species. The GWP of the *H. verticillata* (HV) system was the highest, followed by *E. nuttallii* (EN), while *V. natans* (VN), despite its high total N_2O emissions (Figure 3b; Figure 4), presented a relatively lower GWP, indicating a weaker overall warming effect than that of HV and EN, though still significantly higher than that of the CK (Figure 4).

In all treatments, CH_4 was the dominant source of total warming potential, contributing over 97% of GWP, while N_2O con tributed less than 3%. The pattern of cumulative CH_4 emissions (HV > EN > VN > CK) was consistent with the difference in GWP (Figure 2b; Figure 4), confirming that CH_4 is the primary driver of GHG impacts in these aquaculture systems.

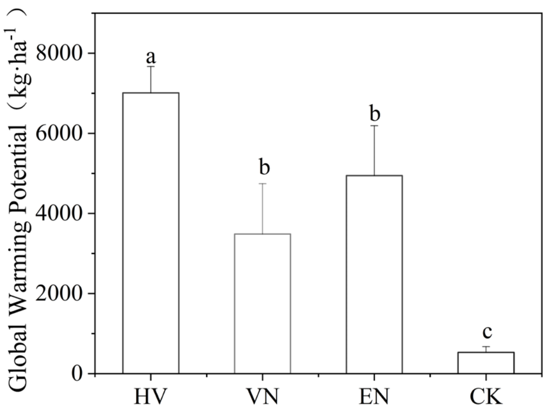


Figure 4. Global warming potential values for each treatment. The bars represent the standard error range, and the same lowercase letter above the bar indicates no statistically significant difference ($p > 0.05$). HV, group with *Hydrilla verticillata*; VN, group with *Vallisneria natans*; EN, group with *Elodea nuttallii*; CK, plant-free control.

3.3. Correlation Between Water Quality Factors and GHG Fluxes

Correlation analysis revealed distinct control patterns for CH_4 and N_2O fluxes [20], with nitrogen-related parameters exerting opposite effects on these two gases (Figure 5a; Figure 5b; Figure 5d; Figure 5e). CH_4 fluxes were negatively correlated with NO_3–N (r = –0.297, $p < 0.05$) and TDS (r = –0.533, $p < 0.01$) (Figure 5a; Figure 5c), but positively correlated with the carbon-nitrogen ratio (C/N) (r = 0.400, $p < 0.05$) (Figure 5b). In contrast, N_2O fluxes showed a strong positive correlation with NO_3–N (r = 0.646, $p < 0.01$) and DO (r = 0.313, $p < 0.05$) (Figure 5d; Figure 5f), but a negative correlation with the C/N ratio (r = –0.318, $p < 0.05$) (Figure 5e). The significant negative correlation between CH_4 and N_2O fluxes (r = –0.260, $p < 0.05$) (Figure 5g) indicates that an increase in one gas may suppress the emission of another under different treatment conditions. To sum up, nitrogen-related factors have opposite effects on CH_4 and N_2O fluxes, which are inversely related to each other.

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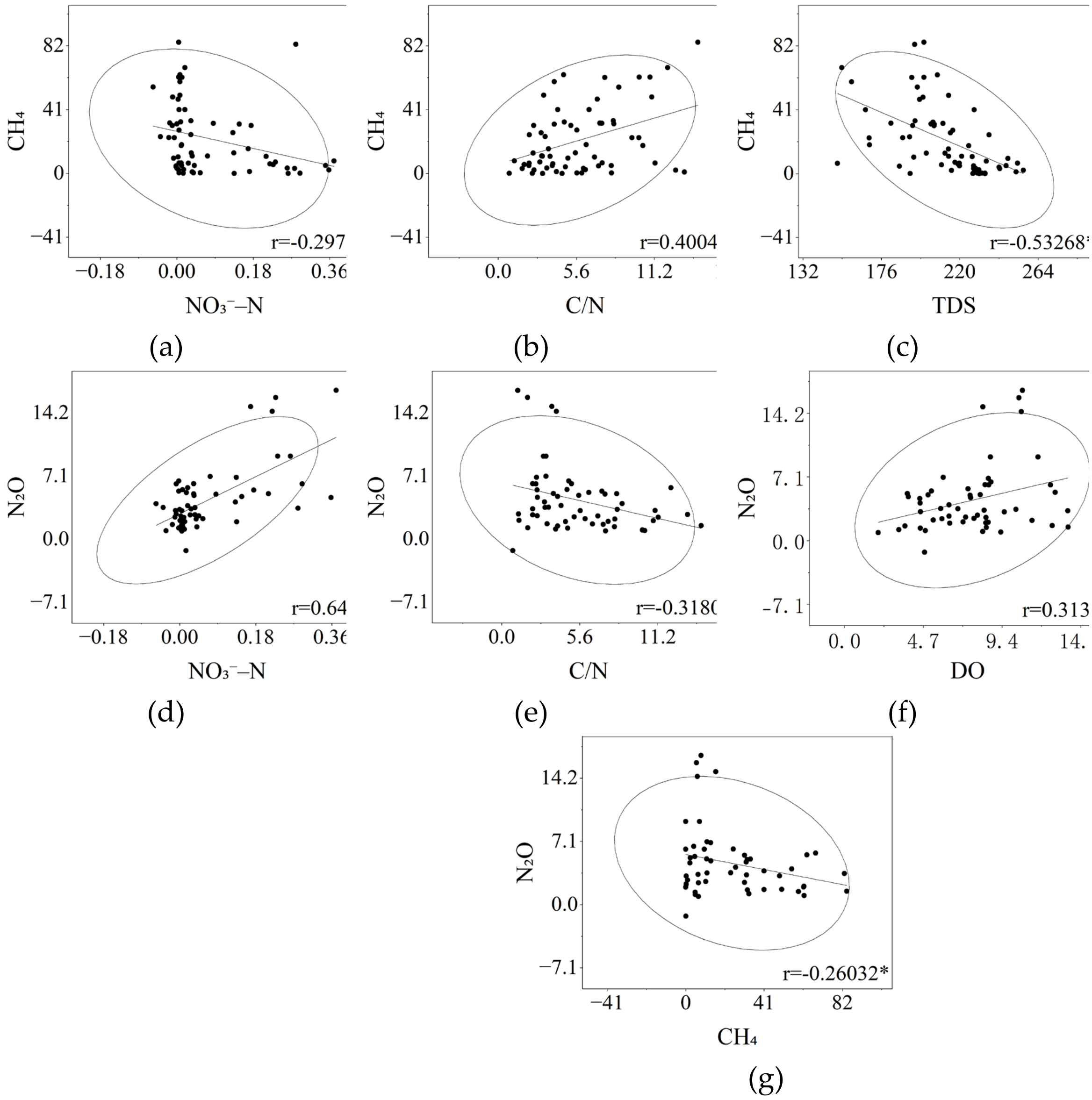

Figure 5. The scatter plot illustrates the relationship between key water quality parameters and greenhouse gas (GHG) emissions. Ellipses represent 95% confidence intervals, and solid lines indicate fitted regression curves. The correlation coefficient (r) is calculated using the Pearson product-moment correlation coefficient. Only parameters with significant correlations are shown in the plot: (a) NO_3–N concentration versus CH_4 flux; (b) C/N ratio versus CH_4 flux; (c) total dissolved solids (TDS) versus CH_4 flux; (d) NO_3–N concentration versus N_2O flux; (e) C/N ratio versus N_2O flux; (f) dissolved oxygen (DO) versus N_2O flux; (g) CH_4 flux versus N_2O flux. * $p < 0.05$, ** $p < 0.01$.

4. Discussion

4.1. Species-Specific Controls of CH_4 Emissions

Submerged macrophytes exert a strong control over CH_4 emissions in aquaculture systems by influencing sediment oxygena tion, root exudation, and microbial activity [21]. In this study, all submerged macrophyte treatments enhanced CH_4 flux compared to the unvegetated control (Figure 4), indicating that the presence of plants typically promotes methanogenesis by increasing labile carbon availability and providing transport pathways for CH_4 diffusion [3,12]. However, significant species-specific differences were observed among HV, EN, and VN. HV exhibited the highest CH_4 emissions, likely due to its extensive aerenchyma and dense canopy structure, which enhance sediment methanogenesis and facilitate CH_4 release to the water surface [22]. EN showed moderate

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CH_4 fluxes, indicating that methanogenesis was partially suppressed through better sediment oxygenation and less effective gas transport pathways. VN exhibited the lowest emissions among the vegetated groups, possibly due to its scattered distribution and weak aerenchyma, which limits plant-mediated CH_4 transfer [23].

In addition, submerged macrophytes influence microbial and planktonic communities, indirectly affecting gas dynamics [24]. The broad leaf surfaces of HV and EN support the growth of dense periphyton and algal biofilms [14]. These communities increase organic matter input through detritus and microbial turnover, stimulating methanogenesis under oxygen-limited conditions [3,15]. In contrast, the smaller leaf surfaces and sparser canopies of VN reduce algal colonization and organic deposition, thus leading to lower CH_4 production. Therefore, the observed emission differences can be attributed to plant morphology, aerenchyma-mediated transport efficiency, and the extent of algal and microbial colonization [24].

4.2. Mechanisms Underlying CH_4 and N_2O Emission Patterns

Although CH_4 and N_2O exhibit opposite temporal patterns, their production mechanisms are interconnected through shared environmental controls [25]. Both gases are regulated by Eh, DO, and nitrogen availability [4]. The negative correlation between CH_4 and NO_3^--N observed in this study suggests that elevated nitrate concentrations inhibit methanogenesis via competitive electron acceptance and stimulation of denitrification [26]. Conversely, higher CH_4 emissions occur under low NO_3^--N and high C/N conditions, consistent with enhanced anaerobic metabolism in carbon rich sediments [8].

The positive correlation between N_2O and NO_3^--N and DO indicates that incomplete denitrification is the main source under sub oxic conditions [4]. Among all treatments, the VN treatment showed the highest N_2O emissions, likely due to sediment disturbance and fluctuations in the redox gradient favoring partial denitrification [16]. In contrast, HV and EN, due to their greater root oxygen release, may promote complete denitrification to generate N_2, thus reducing N_2O accumulation [27]. These findings are consistent with broader aquatic studies suggesting that macrophyte species regulate GHG emissions through complex feedback loops between oxygen transport, nitrogen cycling, and carbon supply [28,29].

4.3. Management Implications and Broader Perspectives

Although submerged vegetation typically enhances GHG emissions compared with the unvegetated control (Figure 4), their ecological functions, such as improving water quality, stabilizing sediments, and supporting crab growth, make them crucial in aquaculture [30]. Therefore, the goal should be not to eliminate macrophytes, but rather to identify optimal species and management strategies to minimize emissions while maintaining ecosystem function. According to this study, *V. natans* appears to offer the most balanced outcomes, with relatively low CH_4 and N_2O fluxes among vegetated treatments. Selecting species with low aerenchyma, moderate canopy density, and controlling planting area can effectively reduce GHG emissions in *E. sinensis* culture systems [31].

Beyond aquaculture, these findings contribute to understanding the mechanisms of carbon-nitrogen coupling and GHG regulation in vegetated wetlands and shallow-water ecosystems. Similar processes exist in natural lakes and restored wetlands, where plant species composition significantly influences sediment carbon turnover and CH_4 transport. Therefore, incorporating species-specific traits into emission models can improve regional and global GHG inventories, thereby supporting climate-smart aquatic management strategies that align with IPCC [1] mitigation goals.

5. Conclusions

This study demonstrates that the cultivation of submerged macrophytes significantly enhanced GHG emissions in *E. sinensis* aquaculture systems, with significant species-specific differences.

Among the plants tested, *H. verticillata* exhibited the highest CH_4 and overall GWP, followed by *E. nuttallii*, while *V. natans* produced the lowest emissions among vegetated treatments. The relatively low GWP of *V. natans* can be attributed to its moderate root oxygen release, weak aerenchyma-mediated gas transport, and low algal attachment, which collectively suppressed methanogenesis and facilitated CH_4 oxidation. These findings indicate that while the presence of macrophyte typically promotes GHG release compared to unvegetated systems, selecting species such as *V. natans* can effectively mitigate emissions while maintaining ecological and productive benefits. Therefore, optimizing plant composition and density in crab aquaculture represents a practical approach that balances productivity and climate-friendly management of aquatic ecosystems.

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Conflicts of Interest: The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Abbreviations

The following abbreviations are used in this manuscript:

GHG	greenhouse gas
CH_4	methane
N_2O	nitrous oxide
GWP	global warming potential
HV	group with *Hydrilla verticillata*
VN	group with *Vallisneria natans*
EL	group with *Elodea nuttallii*
CK	plant-free control
TN	total nitrogen
TP	total phosphorus
NO_3^-–N	nitrate nitrogen
TOC	total organic carbon
DO	dissolved oxygen
WT	water temperature
TDS	total dissolved solids
Chl	chlorophyll
C/N	carbon-nitrogen ratio

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