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Sedimentary Nitrate Respiration Potentially Offsets the Climatic Benefits From CO₂ Uptake by Marginal Seas

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Key Points:

- Temperature and organic carbon (OC) determine spatiotemporal distribution of sediment denitrification and N₂O production in marginal seas
- Denitrification removes 2.8 ± 0.4 Tg N yr⁻¹ in China's marginal seas based on our extrapolation, accounting for 26.5% of external input
- Sediment nitrate respiration consumes OC and releases N₂O simultaneously, counter-balancing $15.1 \pm 8.1\%$ of the air-sea CO₂ uptake

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Sediment nitrate respiration eliminates reactive nitrogen (Nr) and consumes organic carbon (OC) accompanying by CO₂ and N₂O production to partially neutralize the climate benefit of sedimentary carbon burial. The quantitative linkage between carbon and nitrogen stoichiometry and greenhouse potential of this syndepositional process, particularly at a marginal sea scale, remains unexplored. Here we show that temperature and organic matter co-regulate the sediment nitrate respiration and associated N₂O production in China's marginal seas. By establishing empirical equations, we access that 2.8 ± 0.4 Tg Nr (~26.5% of riverine input) is annually respired via degrading 2.2 ± 0.2 Tg OC (~12.5% of OC deposited) to produce 15.0 ± 3.5 Gg N₂O-N, which may counter-balance $15.1 \pm 8.1\%$ of the air-sea CO₂ influx. This link between anthropogenic Nr input and removal to carbon sequestration reveals that sedimentary nitrate respiration potentially reduces the climatic benefits of marginal seas.

Plain Language Summary Sediment denitrification plays a critical role in maintaining Nr balance in aquatic ecosystems, but it can also produce a negative climate feedback via organic matter decomposition and N₂O release. However, the environmental and climatic effects of sediment denitrification, particularly at a continental shelf scale, are still unclear. According to our field investigation in China's marginal seas, we find that sediment denitrification and associated N₂O production are co-regulated by temperature and organic matter. Extrapolation results based on empirical equations indicate that sediment denitrification removes 2.8 ± 0.4 Tg N yr⁻¹ in China's marginal seas, accounting for 26.5% of riverine input. Meanwhile, approximately 2.2 ± 0.2 Tg C yr⁻¹ of organic carbon is consumed and 15.0 ± 3.5 Gg N yr⁻¹ of N₂O is produced along with sediment denitrification, collectively counter-balancing $15.1 \pm 8.1\%$ of the air-sea CO₂ influx. These findings reveal that sedimentary nitrogen removal potentially offsets the climatic benefits of carbon uptake in marginal seas.

1. Introduction

Marginal seas are critical receptors and burial centers of both terrestrial and marine organic carbon (OC), collectively accounting for more than 90% of sedimentary OC burial in marine environments (Bianchi et al., 2018; Burdige, 2005), and serving as an important component in climate systems on various timescales. In marginal seas, the input of anthropogenic reactive nitrogen (Nr) alleviates nitrogen limitation of primary production, and results in an enhanced OC export to sediments (Moore et al., 2013). However, only a fraction of the deposited organic matter that escapes from respiratory consumption can represent the carbon sink in sediments. As oxygen runs out, nitrate respiration, the most important sediment Nr removal process, takes on the responsibility to consume organic matter. Thus, these carbon and nitrogen biogeochemical cycles in marginal seas are tightly coupled not only via anthropogenic Nr induced additional OC production, but also by OC deposition-enhanced Nr removal in sediments. However, large excesses of anthropogenic Nr input perturb the homeostasis of the ocean and alter pristine nitrogen transformations and the coupled carbon biogeochemical cycle (Greaver et al., 2016; Gruber & Galloway, 2008). Since sedimentary Nr removal is one of the important processes maintaining the balance of the Earth system and more than 50% of Nr removal occurs in marginal seas (Bohlen et al., 2012), the correlation between sedimentary nitrogen and carbon removal in marginal seas needs to be quantified, particularly, in the perspective of greenhouse potential.

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Heterotrophic denitrification is the main nitrate respiration pathway in sediments along with OC consumption and nitrous oxide (N_2O , ~300 times more potent than carbon dioxide in term of warming potential) production (Tiedje et al., 1982). Nitrate respiration impairs carbon sequestration capacity because the carbon respired is not buried, and combined with N_2O release results in a positive climatic feedback (Wan, Sheng, et al., 2022). In contrast, anaerobic ammonium oxidation (anammox), a relatively newly discovered Nr removal process (Devol, 2015), eliminates Nr and involves chemoautotrophic carbon fixation but no N_2O production (Kartal et al., 2013; Strous et al., 1999). Both denitrification and anammox are microbially mediated but accompanied by distinctive climatic and biogeochemical impacts. The environmental factors governing Nr removal across climatic gradients have been reported in soils, rivers and wetlands (Hou et al., 2015; Li et al., 2019, 2020). However, how sedimentary Nr removal affects carbon sequestration and greenhouse gases production in marginal seas at a continental scale is poorly constrained due to the limited number and areal coverage of field observations.

In a nutshell, the biological pump mitigates the atmospheric CO_2 , while the settled fresh organic matter may promote sediment nitrate respiration and associated CO_2 and N_2O production to weaken the carbon sink in marginal seas. This series of inherent carbon and nitrogen stoichiometry link the carbon-nitrogen biogeochemical cycles to greenhouse gases budget throughout the atmosphere-water column-sediment continuum, but lack of a quantitative assessment for a larger spatial scale. Establishing empirical equations between biogeochemical rates and key environmental factors is one of the ways for extrapolation and assessment (Rocher-Ros et al., 2023; Sun et al., 2021).

China has a long coastline that hosts large coastal and shelf seas (Figure 1a showing geographical location). The Nr input to the Bohai Sea (BS) and Yellow Sea (YS) has increased four times from 0.9 to 3.8 Tg N yr⁻¹ during 1970–2010. In the same period, the Nr input into the East China Sea (ECS) and the Northern South China Sea (NSCS) increased from 1.1 to 5.0 Tg N yr⁻¹ and from 1.7 to 4.7 Tg N yr⁻¹, respectively (Wang et al., 2020). In addition, the average values of total organic carbon (TOC) deposition fluxes to sediments for the last 20 years in BS/YS, ECS, and NSCS were 5.6, 7.4, and 4.8 Tg C yr⁻¹, respectively (Jiao et al., 2018). Integrating these reports on Nr input and OC deposition allows us to assess the effect of nitrate respiration on marginal sea carbon sink. By applying the ¹⁵N isotope pairing technique (Hsu & Kao, 2013) to sediments distributed from subtropical to temperate zones along the coast of China (Figure 1a), including the Jiulong River Estuary (JRE), Sansha Bay (SB), Yangtze River Estuary (YRE) and BS, we quantified the denitrification and anammox-associated gaseous potential production rates (N_2 and N_2O). Combining the historical observations in China's marginal seas, empirical equations have been developed to link N removal and N_2O production with fundamental physico-chemical parameters to derive the spatiotemporal distribution of sedimentary denitrification and associated N_2O production at a marginal sea scale. Moreover, we quantitatively assess the effects of sedimentary nitrate respiration on the carbon sink function of China's marginal seas.

2. Materials and Methods

2.1. Sampling and Pretreatment

Sampling cruises were conducted from 24 to 31 May 2017 in the BS, from 21 July to 6 August 2017 in the YRE and from 26 to 28 July 2019 in the SB (Figures 1b–1d), representing the summer season. While in the JRE, samples were collected along the salinity gradient during four cruises conducted in spring (20 April 2017), summer (20 July 2018), autumn (4 September 2016) and winter (16 December 2015) (Figure 1e). Near-bottom water and surface sediments (1 cm) were collected at each sampling site using a 5 L Niskin bottle and a grab sampler, respectively. For water samples, ~1 L of bottom water was filtered with a 0.22 μm polycarbonate membrane, and then one part of the filtrate was stored at –20°C for ammonium (NH_4^+) and nitrite plus nitrate (NO_x^-) analysis, while the remaining filtrate was prepared for slurry incubation. Moreover, the surface sediments were divided into two parts: one was stored at –20°C for the measurement of sediment porosity, the contents of OC and organic nitrogen (ON); the other part of sediments was applied to conduct slurry incubation experiments.

2.2. Nitrogen Removal Rate Determination and Extrapolation

The potential rates of nitrogen removal processes and associated N_2O production in surface sediments were measured via slurry incubation (Tan et al., 2020; Thamdrup & Dalsgaard, 2002). See detailed information for rate determination in Supplementary Materials and Methods in Supporting Information S1. The potential rates were calibrated according to the relationship between potential and in situ rates. Integrating our results into historical

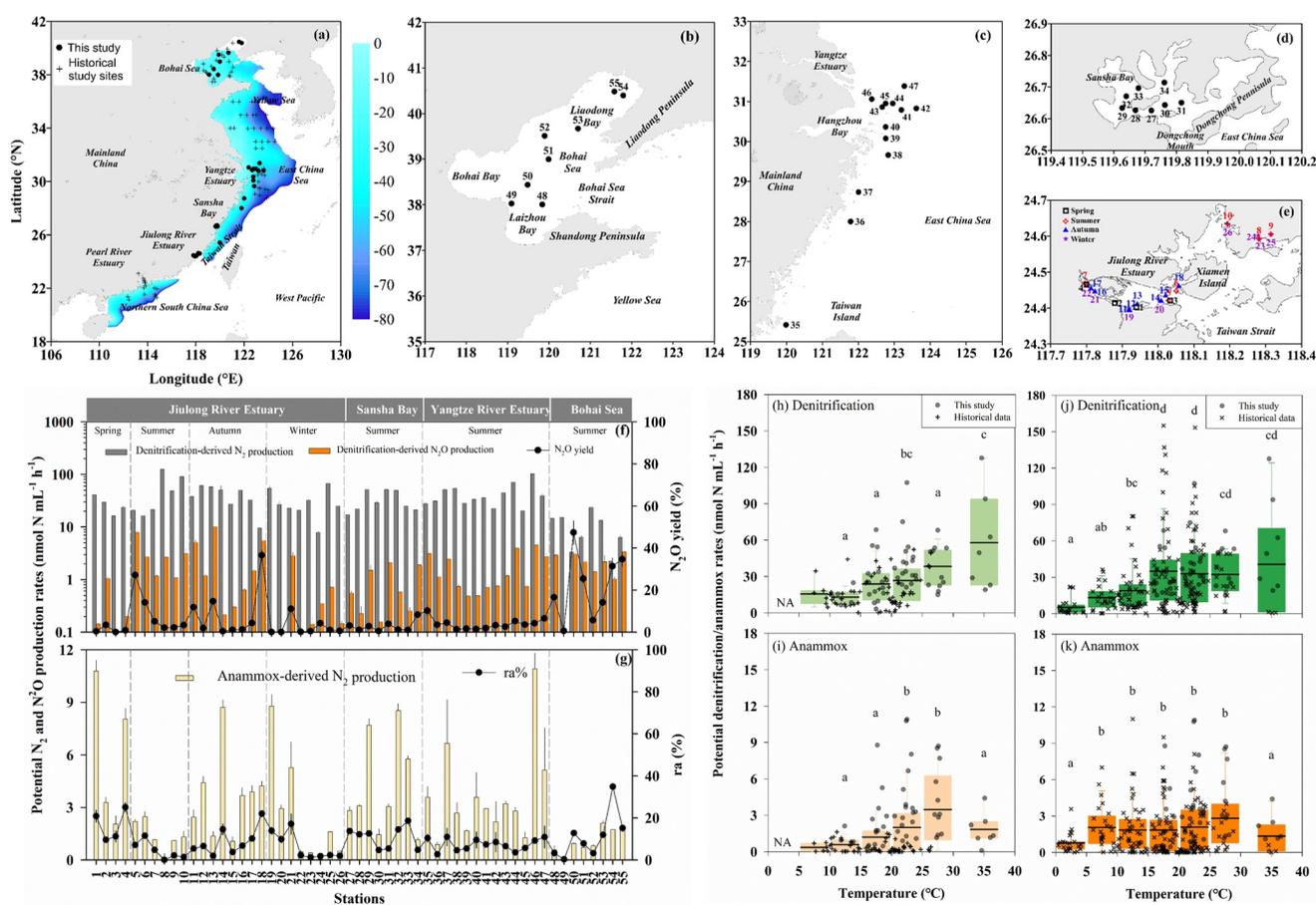


Figure 1. Location of sampling sites (a–e), spatiotemporal variability of sediment denitrification/anammox, (f and g) in China's marginal seas, and their interaction with temperature from this study, (h and i) and historical researches including our data, and (j and k). All sampling sites from this study are annotated using numbers from low to high latitudes. The color bar shows the water depth of <80 m. Different seasons are separated by vertical dotted lines in (f). Error bars represent the standard deviation of triplicates. All data in (h)–(k) are listed in Supplementary Table S2 in Supporting Information S1. Significant differences ($p < 0.05$) among the groups are indicated as different letters on the boxes in (h–k). NA represents not applicable.

observations in China's marginal seas, the empirical relationships between biogeochemical rates and environmental factors (Supplementary Table S1 in Supporting Information S1) were achieved by using a stepwise multiple linear regression approach (McCalley et al., 2014). The empirical equations were applied to extrapolate the sedimentary denitrification and associated N₂O production rates in YS/BS, ECS, and NSCS (See detailed descriptions in Supplementary Materials and Methods in Supporting Information S1).

2.3. Statistical Analysis

The stepwise regressions were conducted using Statistical Package of Social Sciences (SPSS, version 26). One-way analysis of variance is performed to examine the variation in denitrification and anammox potential rates in different zoned temperature groups by using the SPSS (version 26) at a 0.05 significance level. The regression lines between nitrogen removal rates and environmental factors are fitted using SigmaPlot 12.5.

3. Results and Discussion

3.1. Sedimentary Denitrification, Anammox, and Associated N₂O Production

Potential sedimentary denitrification rates varied from 3.2 to 127.7 nmol N mL⁻¹ h⁻¹ for the studied seasons and areas (Figure 1f). These sediment denitrification potentials ranged over three orders of magnitude, but our measurements are within the reported range including estuarine and continental shelf sediments, and inland river and wetland sediments (Supplementary Table S2 in Supporting Information S1). Although anammox occurs

widely in Chinese coastal sediments, the potential rates of anammox were 1–2 orders of magnitude lower than those of denitrification, ranging from 0 to $10.9 \text{ nmol N mL}^{-1} \text{ h}^{-1}$ (Figure 1g). These observed anammox rates are in line with literature reports for sediments or soils (Supplementary Table S2 in Supporting Information S1). Overall, our findings revealed that denitrification predominates sedimentary N_r removal accounting for ~91% to total nitrogen loss. In contrast, anammox made a minor contribution with an average of $8.8 \pm 6.8\%$ (0.1%–34.9%; Figure 1g), which are comparable to historical researches in similar coastal environments but is largely lower than those in deep sea sediments (Supplementary Table S2 in Supporting Information S1).

Our observations show that sedimentary denitrification-derived N₂O production ranged from 0.2 to $10.0 \text{ nmol N mL}^{-1} \text{ h}^{-1}$ with N₂O yields of 0%–47.4% (Figure 1f), similar to the limited literature reports for sediments from different habitats (e.g., 13%–64% in Lake Nätstjärn (Myrstener et al., 2016) and 2%–62% in Yangtze lakes (Liu et al., 2015)). On average, $7.2 \pm 10.5\%$ of the removed nitrogen flows toward N₂O regardless of season and region, which is higher than our in situ data (average of $1.8 \pm 2.2\%$) in the JRE and YRE (Tan et al., 2022). According to our limited observations, the potential N₂O yield was roughly 11.2-fold higher than in situ yield (See detail comparison in Supplementary Materials and Methods and Figure S9 in Supporting Information S1). Due to the high nitrate availability in slurry incubation, denitrification preferably run until N₂O as the reduction from nitrate to N₂O is energetically more favorable than the complete reduction to dinitrogen (Richardson et al., 2009), thereby resulting in a higher potential N₂O yield.

3.2. Regulation of Temperature and Organic Matter on Sediment Nitrogen Transformations

The correlation analysis between the biogeochemical rates with the observed environmental factors (see details in Supplementary Results in Supporting Information S1, Table S1 in Supporting Information S1 and Figure S1 in Supporting Information S1) showed that temperature and organic matter were largely responsible for the spatiotemporal distribution of sediment nitrate respiration and related N₂O production along the coast of China (Supplementary Table S3 in Supporting Information S1).

Temperature is a fundamental environmental factor governing microbial activities on Earth. In general, temperature directly affects the microbial metabolism, and thus denitrification and anammox rates change as temperature changes (Brin et al., 2017; Tan et al., 2020). The majority of local field observations reported in the literature revealed that temperature plays a crucial role in shaping the biogeographical distribution of the nitrogen removal processes in sediments (Brin et al., 2014; Tan et al., 2017). In addition, site-specific temperature manipulation experiments have shown that rising temperature facilitates the activities of denitrifying and anammox bacteria though with different optimal temperatures (Canion, Kostka, et al., 2014; Tan et al., 2020).

To further explore the thermal response of denitrification and anammox at an ecosystem level, the potential rates of these two nitrogen removal pathways and the corresponding habitat temperatures from China's marginal seas and different aquatic ecosystems globally have been compiled (Supplementary Table S2 in Supporting Information S1). All data from this study (Figures 1h and 1i) and available observations including historical and our results (Figures 1j and 1k) were binned into seven groups with a habitat temperature width of 5°C. For data from the Chinese seas, the average denitrification potential shows increasing with temperature over the range of 5–35°C (Figure 1h). Average anammox potential rates increase as well up to temperatures of 5–30°C, but then decrease significantly toward higher temperatures (>30°C, Figure 1i). Integrating our results with literature data, denitrification still increases with increasing temperature over the range of 0–20°C, but above 20°C, denitrification rates stable at a high level till 35°C (Figure 1j), while anammox rates showed a relatively flat thermor-
response over the range 5–30°C (Figure 1k).

Based on the compiled data (Supplementary Table S2 in Supporting Information S1), we obtain exponential regression functions for the potential rates of the two nitrogen removal pathways against temperature (Supplementary Figure S2 in Supporting Information S1). After transferring these obtained fitting curves by using the method described in (Zheng et al., 2017), we find a higher temperature response (Q_{10}) for denitrification (1.39–2.52, Supplementary Figure S2a in Supporting Information S1) than that for anammox (1.27–1.99, Supplementary Figure S2b in Supporting Information S1). Moreover, the global compilation of percent anammox and temperature indicates that ra% is strongly and negatively correlated to temperature (Supplementary Figure S2c in Supporting Information S1), strongly suggesting that climate-friendly anammox bacteria will become less competitive under warming stress due to their weakened metabolic responses to higher temperatures (Tan et al., 2020). These synthesis results reveal that anammox bacteria are relatively psychrotolerant, while

denitrifiers have a thermotolerant ecological niche, leading to a stronger resilient adaptability in the ongoing warming world. The community-level thermos-response obtained from temperature manipulation experiments from different latitudes (Brin et al., 2017; Canion, Overholt, et al., 2014; Tan et al., 2020) showed consistent results with individual observations in the field across ecosystems.

Our data showed that sedimentary denitrification-induced N_2O production depends on temperature at both seasonal and spatial scales (Supplementary Table S3 in Supporting Information S1), consistent with field observations and manipulation experiments showing that rising temperature stimulates the release of denitrification-derived N_2O (Myrstener et al., 2016; Tan et al., 2020; Velthuis & Veraart, 2022). In fact, N_2O production represents an integral response since multienzymatic reactions are involved in N_2O generation/consumption during nitrate respiration (Kuypers et al., 2018), and the temperature effects on each individual step may be distinct. N_2O can be produced via direct denitrification and coupled nitrification-denitrification, however, slurry incubation cannot distinguish N_2O production pathways and represents a potential capacity, resulting in an overestimation of N_2O production to a certain extent. Further studies are needed to explore the underlying mechanisms of N_2O release and its thermal responses in aquatic environments. Collectively, global warming induces more nitrogen flow toward nitrate respiration, thus concomitantly facilitates denitrification-induced OC oxidation and N_2O release, potentially resulting in a positive climate feedback (Canion, Overholt, et al., 2014; Dalsgaard & Thamdrup, 2002; Tan et al., 2020).

In addition, organic matter is another important regulator for nitrogen loss, consistent with many studies showing that denitrification is largely controlled by the availability of organic matter in coastal systems (Albert et al., 2021; Bartl et al., 2019; Huang et al., 2022; Piña-Ochoa & Álvarez-Cobelas, 2006). Our results revealed that sediments with higher contents of OC and ON, and lower C/N ratios support denitrification in China's marginal seas (Supplementary Table S3 in Supporting Information S1 and Figure S3 in Supporting Information S1), suggesting that both the quantity and quality of organic matter have great impacts on sedimentary nitrate respiration. It is well known that organic matter serves as the substrate and energy source for heterotrophic denitrifiers. Labile organic matter yields more respiration energy and supports more biomass growth, and thus promotes nitrate respiration in sediments (Strohm et al., 2007).

The quantity and quality of organic matter determine whether the products of sediment denitrification flow towards N_2O or N_2 . The negative correlation between N_2O yield and the contents of OC and ON (Supplementary Table S3 in Supporting Information S1) indicates that abundant organic matter is conducive to complete denitrification and thus promotes N_2O reduction. In addition, the significant positive correlation between N_2O yield and C/N ratio (Supplementary Table S3 in Supporting Information S1) strongly suggests that relative refractory organic matter with high C/N favors N_2O production during sediment denitrification. This regulation of organic matter quality on N_2O production is also supported by Lin et al. (2017), who found that the N_2O/N_2 ratio during sedimentary denitrification was positively correlated to terrestrial OC with high C/N. Such a result implies that organic matter with low quality may lead to incomplete denitrification, resulting in a higher proportion of nitrogen flowing toward N_2O release.

3.3. Upscaling of Sedimentary Nitrate Respiration and Its Greenhouse Effect

According to the empirical equations (Supplementary Tables S4 and S5 in Supporting Information S1), we estimate sediment denitrification and N_2O yield in the BS/YS, ECS/Taiwan Strait (ESC/TS), and NSCS in China's marginal regions with water depths of shallow than 80 m (Supplementary Figure S4a in Supporting Information S1). The predicted denitrification rates ranged from 0.1 to 1.9 $mmol N m^{-2} d^{-1}$, showing spatial and seasonal variations (Figures 2a–2d). High temperature, high OC and ON content, and low C/N (Supplementary Figures S4 and S5 in Supporting Information S1) synergistically result in relative high sediment denitrification activities in the nearshore of the NSCS throughout four seasons (Figures 2a–2d). While low denitrification occurred in the BS/YS particularly in spring and winter (Figures 2a and 2d) mainly due to the low substrate concentration and temperature (Supplementary Figures S4 and S5 in Supporting Information S1). Evidently, latitudinal gradients are driven by seasonal temperature distributions, particularly in spring and winter (higher rates at lower latitudes; Figure 2e). The seasonality in sedimentary denitrification was highest in the BS/YS, followed by the ESC/TS, while the seasonal pattern in the NSCS was not evident due to less variable bottom-water temperatures at low latitude (Figure 2f). This seasonal pattern indicates that temperature is a major environmental factor governing biogeochemical processes in coastal margins at mid-high latitudes.

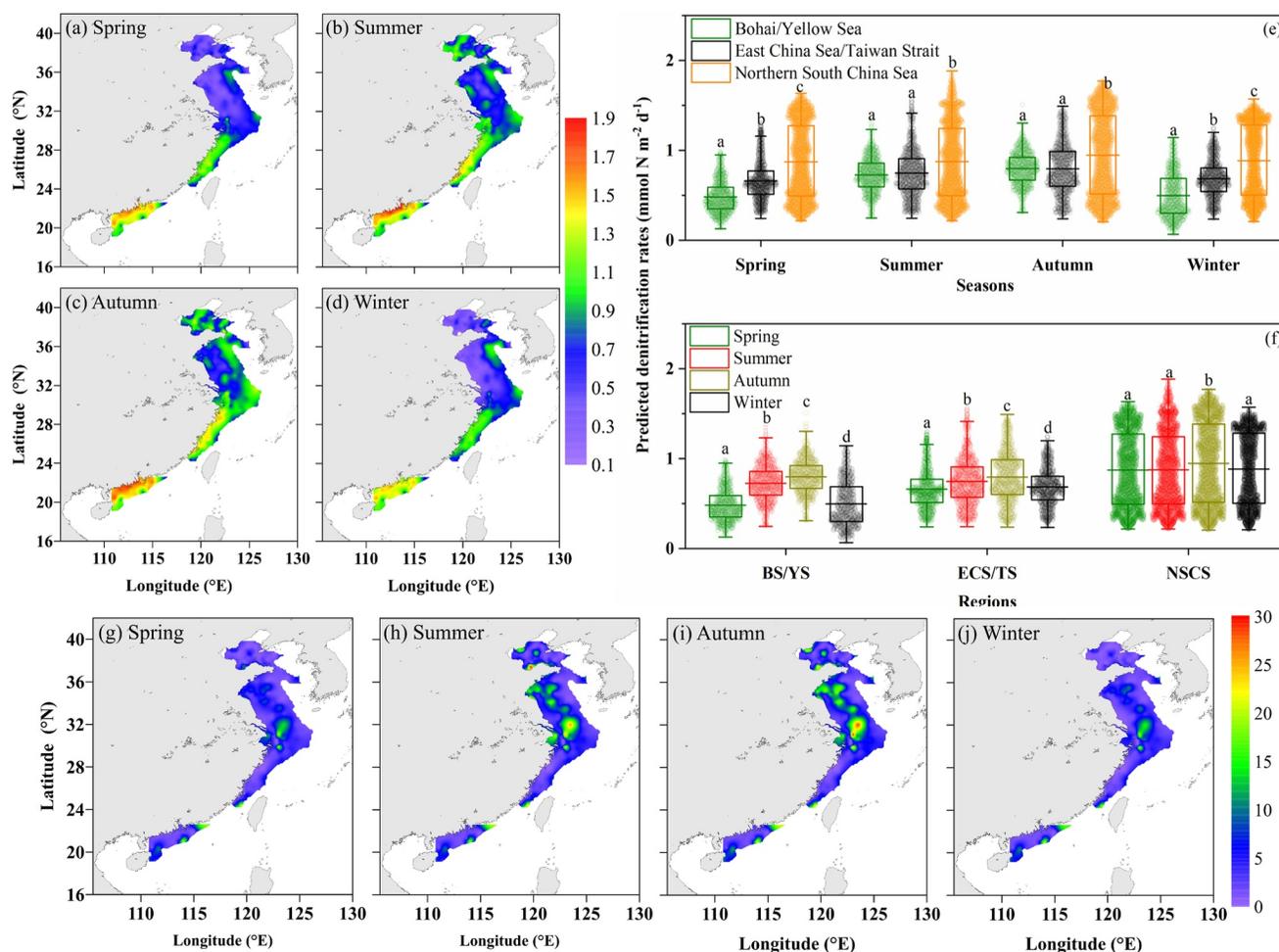


Figure 2. The seasonal spatial distributions of sediment denitrification (a–f, unit in $\text{mmol N m}^{-2} \text{d}^{-1}$) and N_2O production (g–j, unit in $\mu\text{mol N m}^{-2} \text{d}^{-1}$) in the marginal seas of China. Significant differences among the groups are indicated as different letters on the boxes ($p < 0.05$).

The predicted N_2O yield in China marginal seas ranged from 0.01% to 4.8% (Supplementary Figure S6a in Supporting Information S1). Next, the denitrification-induced N_2O production rate was calculated by multiplying the projected denitrification rate with the N_2O yield at the corresponding site (Figures 2g–2j). The areal N_2O production rate was usually less than $5 \mu\text{mol N m}^{-2} \text{d}^{-1}$ but with patches having emission rates as high as 20–30 $\mu\text{mol N m}^{-2} \text{d}^{-1}$, particularly off the YRE (Figures 2g–2j). Our annual estimates in BS/YS ($4.5 \pm 3.9 \mu\text{mol N m}^{-2} \text{d}^{-1}$), ECS/TS ($5.3 \pm 4.1 \mu\text{mol N m}^{-2} \text{d}^{-1}$), and NSCS ($4.8 \pm 4.3 \mu\text{mol N m}^{-2} \text{d}^{-1}$) account for 32%, 52%, and 87% of the observed sea-air effluxes in the corresponding regions, such as $14.2 \pm 9.4 \mu\text{mol N m}^{-2} \text{d}^{-1}$ in BS/YS (Gu et al., 2022), $10.2 \pm 15.4 \mu\text{mol N m}^{-2} \text{d}^{-1}$ in ECS/TS (Chen et al., 2021), and $5.5 \pm 3.9 \mu\text{mol N m}^{-2} \text{d}^{-1}$ in NSCS (Tseng et al., 2016; Wan, Lin, et al., 2022). Such results indicate that sedimentary N_2O production has the potential to contribute much to sea-air effluxes.

The areal biogeochemical rates from four seasons were integrated to compute annual sedimentary nitrogen removal and associated N_2O emission fluxes (Supplementary Materials and Methods in Supporting Information S1). The annual total nitrate respiration fluxes are estimated to be 1.0 ± 0.1 , 1.0 ± 0.1 , and $0.6 \pm 0.1 \text{ Tg NO}_3\text{-N yr}^{-1}$ for BS/YS, ECS/TS and NSCS, respectively. Based on a mol-based C to N quotient of 0.88 during denitrification (Gruber, 2008), nitrate respiration-induced OC decomposition is calculated to be 0.87 ± 0.11 , 0.85 ± 0.10 , and $0.50 \pm 0.04 \text{ Tg C yr}^{-1}$, accounting for $15.6 \pm 1.9\%$, $11.5 \pm 1.3\%$, and $10.5 \pm 0.8\%$ of TOC deposition fluxes (Jiao et al., 2018) in corresponding seas (Figure 3 and Supplementary Table S6 in Supporting Information S1). However, this denitrification-derived carbon decomposition can be compensated, to a small extent, by CO_2 fixation through autotrophic anammox. On average, nitrate respiration consumed $12.5 \pm 1.4\%$ of

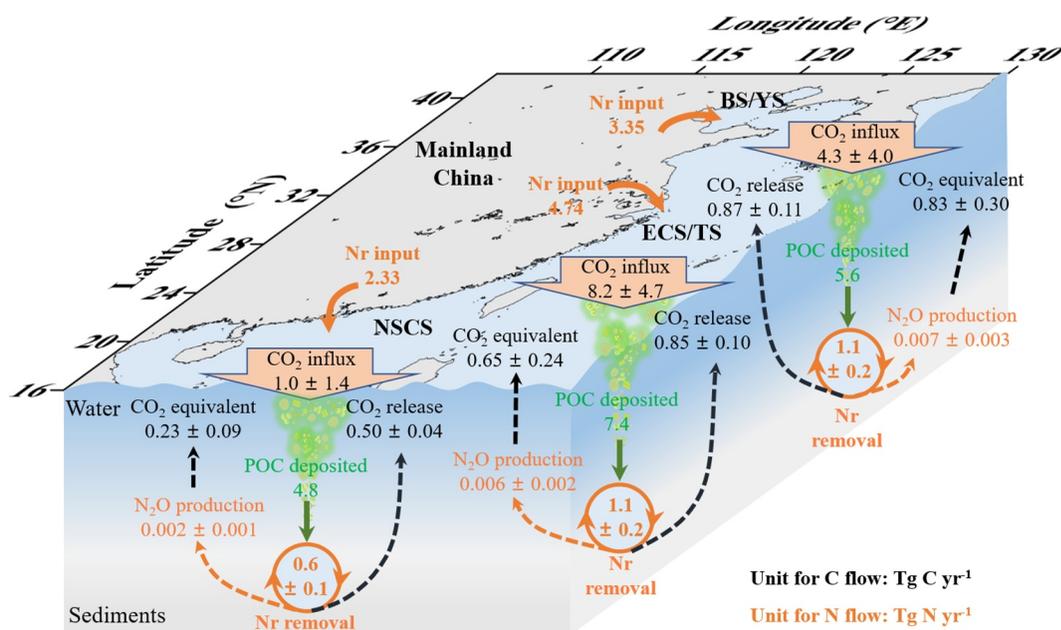


Figure 3. The conceptual diagram of sediment nitrate respiration-derived carbon and nitrogen coupled biogeochemical cycles in China marginal seas. Bohai Sea/Yellow Sea (YS), East China Sea (ECS)/TS, and Northern South China Sea (NSCS) represent the Bohai/YS, ECS/Taiwan Strait, and NSCS, respectively. The orange and black arrows indicate N and C flows, respectively.

TOC deposition flux in China's marginal seas. Dissimilatory nitrate reduction to ammonium (DNRA) is another nitrate reduction process which consumes OC in sediments. Limited studies have indicated that DNRA accounts for 1%–45% of nitrate reduction in estuarine sediments with high spatiotemporal variabilities (Deng et al., 2015; Gao et al., 2022; Song et al., 2013), while the relative importance of DNRA to nitrate reduction is still unclear in shelf sea sediments. The effects of DNRA on sediment OC consumption cannot be ignored and needs to be further studied. Finally, nitrate reduction together with aerobic respiration and sulfate reduction contribute largely to sedimentary OC degradation in marginal seas.

Considering the contribution (average $8.8 \pm 6.8\%$) of anammox to nitrogen removal in China coastal sediments, the total Nr removal fluxes in BS/YS, ECS/TS and NSCS are calculated to be 1.1 ± 0.2 , 1.1 ± 0.2 , and 0.6 ± 0.1 Tg N yr⁻¹, accounting for $32.3 \pm 4.7\%$, $22.3 \pm 3.1\%$, and $26.7 \pm 2.9\%$ of the total nitrogen input to the corresponding seas, respectively (Figure 3 and Supplementary Table S6 in Supporting Information S1). In total, approximately 2.8 ± 0.4 Tg N yr⁻¹ is removed in China's marginal seas, which is equivalent to $26.5 \pm 3.6\%$ of the annual total Nr input (Supplementary Table S6 in Supporting Information S1). This finding emphasizes the important function of shelf sea sediments in eliminating riverine reactive nitrogen.

During nitrate respiration, approximately 7.30 ± 2.65 , 5.76 ± 2.11 and 1.98 ± 0.84 Gg N yr⁻¹ of removed nitrogen flow toward N₂O production in BS/YS, ECS/TS and NSCS, respectively (Figure 3 and Supplementary Table S6 in Supporting Information S1). This produced N₂O can be further reduced to dinitrogen by denitrifying bacteria in substrate deficient sediments (Wankel et al., 2017) and even in oxygenated waters (Tang et al., 2022), thus alleviating greenhouse gas emission. However, N₂O can also be produced via both nitrification and denitrification in hypoxic zone (such as hypoxia area off the YRE) and turbid waters (Wan et al., 2023; Zhang et al., 2023). Together with this produced N₂O, the sediment N₂O may reach to overlying waters, and subsequently contribute to sea-air N₂O efflux, particularly in shallow-water systems under the forcing of seasonal mixing and episodic events (such as typhoon and rainstorm), resulting in a crucial climate feedback. If all the produced N₂O is emitted into the atmosphere, then the N₂O fluxes correspond to 0.83 ± 0.31 , 0.65 ± 0.24 and 0.23 ± 0.09 Tg CO₂-eq yr⁻¹ (using a 100 year Global Warming Potential-based weighting of 265) for BS/YS, ECS/TS and NSCS, respectively (Figure 3 and Supplementary Table S6 in Supporting Information S1). These estimates counterbalance 10.1%–26.8% of the annual average sea-air CO₂ influxes in the BS/YS, the ECS/TS and the NSCS with high variability (Supplementary Table S6 in Supporting Information S1). Overall, sediment nitrate

respiration in China's marginal seas produces approximately 15.04 ± 3.49 Gg N yr⁻¹ of N₂O, corresponding to 1.71 ± 0.40 Tg CO₂-eq yr⁻¹, potentially offsetting $15.1 \pm 8.1\%$ of the climatic benefits from total air-sea CO₂ uptake (13.4 ± 6.3 Tg C yr⁻¹; Figure 3 and Supplementary Table S6 in Supporting Information S1). This estimate is reasonable since the latest synthesis of global coastal greenhouse gases has revealed that N₂O and methane emissions offset 30%–60% of carbon uptake in a net radiative balance (Resplandy et al., 2024).

The denitrification prediction showed a consistently low uncertainty (0.01 – 0.1 mmol m⁻² d⁻¹; <15%) in the study regions, with exceptions in the BS and nearshore YS in spring and winter, which have relatively high uncertainties of 30%–60% (Supplementary Figure S7 in Supporting Information S1). While the largest uncertainty (8 – 10 μmol m⁻² d⁻¹; 56%–90%) for N₂O production was observed off the YRE and nearshore BS particularly in summer and autumn (Supplementary Figure S8 in Supporting Information S1), mainly due to the large variations in N₂O yield in these regions (Supplementary Figure S6b in Supporting Information S1). Our upscaling method has weakness and limitations during the establish of empirical equation and then extrapolation. First, we only considered the average conversion factors for the overestimation of both denitrification and N₂O yield (Supplementary Figure S9 in Supporting Information S1). However, the correct of overestimation was based on limited data, the wide range of conversion factors (4.2–13.2 for denitrification and 1.5–30.3 for N₂O yield; Supplementary Figure S9 in Supporting Information S1) can result in large uncertainties for the predictions. The overestimation is depended on the potential and in situ rate/yield, which are regulated by various environmental factors, including temperature, organic matter content, nitrate, and salinity (Tan et al., 2022). Several factors have been accounted for our extrapolation, as our sensitivity analysis indicates that a ±100% of variation in individual OC and ON, temperature, and C/N can lead to a 1-fold of change in denitrification, and a 1–3 folds change in N₂O yield (Supplementary Figure S10 in Supporting Information S1). Second, some other parameters, such as the sediment heterogeneity (texture and grain size) and microbial community structure, which may affect the spatiotemporal distribution of carbon and nitrogen biogeochemical activities, were not taking into account. Third, only N₂O production was observed during slurry incubation, while sediments also consume N₂O (Murray et al., 2015). This N₂O consumption, which is not considered in this study, can partly reduce our estimated N₂O emission. Nevertheless, our study provides a way with an intrinsic logic to quantitatively evaluate the chemometrics of carbon and nitrogen linking their biogeochemical transformations at the water-air interface and sediment-water interface by using all available data at a large spatial scale.

4. Concluding Remarks

This is the first attempt to access sediment nitrate respiration and its net impacts on Nr removal, carbon sequestration and climatic feedback at the continental margin scale. Our findings indicate that nitrate respiration in sediments plays crucial roles in eliminating Nr, and thus the decrease in frequency, duration and intensity of harmful algae blooms in coastal oceans. Meanwhile, sedimentary nitrate respiration has a great potential to offset the climatic benefits of carbon uptake due to OC decomposition and N₂O production, and thus reduce the role of marginal seas as a carbon sink. Accordingly, we propose a framework of nitrogen-carbon coupled biogeochemical cycles in coastal oceans, such a nitrogen-carbon cycle loop involves the transformations of nitrogen and carbon in different phase states (dissolved, particulate and gaseous), and links different biogeochemical processes in atmosphere-water-sediment continuum, contributing to a series of ecological and climatic feedbacks (such as carbon sink, nitrogen removal, greenhouse gas release, etc.), and playing a vital role in maintaining the balance of the Earth's ecological and climatic systems at different time and spatial scales.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

The data from this study and historical studies can be obtained from the Supporting Information S1. In particular, the synthesis data on sediment nitrogen removal from global ecosystems can be found in Mendeley Data (Tan, 2024a). The data set on content of organic matter in surface sediment and bottom water temperature in China's marginal seas can be found in Mendeley Data (Tan, 2024b; Tan, 2025). Temperature and water depth data for equation simulation are retrieved from European Union-Copernicus Marine Service (2016).

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