Global database of actual nitrogen loss rates in coastal and marine sediments

Yongkai Chang[1], Ehui Tan[1*], Dengzhou Gao[2], Cheng Liu[3], Zongxiao Zhang[4], Zhixiong Huang[1], Jianan Liu[1], Yu Han[1], Zifu Xu[1], Bin Chen[5], Shuh-Ji Kao[1*]

[1] State Key Laboratory of Marine Resource Utilization in South China Sea, School of Marine Science and Engineering, Hainan University, Haikou, China

[2] Key Laboratory for Humid Subtropical Eco-Geographical Processes of the Ministry of Education, School of Geographical Sciences, Fujian Normal University, Fuzhou, China

[3] Shandong Key Laboratory of Eco-Environmental Science for the Yellow River Delta, Shandong University of Aeronautics, Binzhou, China

[4] School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, Guangdong, China

[5] State Key Laboratory of Marine Environmental Science, College of Ocean and Earth Sciences, Xiamen University, Xiamen, China

[*]**Corresponding author:**

Ehui Tan (ehuitan@hainanu.edu.cn) and Shuh-Ji Kao (sjkao@hainanu.edu.cn)

Abstract

Denitrification and anaerobic ammonium oxidation (anammox) convert reactive nitrogen to invert N_2, and play vital roles in nitrogen removal in coastal and marine ecosystems, weakening the adverse effects caused by terrestrial excessive nitrogen inputs. Given the importance of denitrification and anammox in nitrogen cycle, lots of studies has measured denitrification and anammox through intact core incubations across different systems, and nitrogen loss processes are affected by a series of environmental factors such as organic carbon, nitrate, dissolved oxygen and temperature. However, a global synthesis of actual nitrogen loss rates is lacking and how environmental factors regulate nitrogen loss remains unclear. Therefore, we have compiled a database of nitrogen loss rates, including denitrification and anammox in coastal and marine systems from published literatures. This database includes 473, 466, and 255 measurements for total nitrogen loss, denitrification and anammox, respectively. This work deepens our understanding of the spatial and temporal distribution of denitrification, anammox and the relative contribution of anammox to total nitrogen loss and their corresponding environmental controls. To our knowledge, the constructed database for the first time offers a comprehensive overview of actual nitrogen loss rates in coastal and marine ecosystems on a global scale. This database can be utilized to compare nitrogen loss rates of different regions, identify the key factors regulating these rates, and parameterize biogeochemical models in the future. This database is available in Figshare repository ： https://doi.org/10.6084/m9.figshare.27745770.v3 (Chang et al., 2024).

KEYWORDS: nitrogen cycle, denitrification, anammox, coastal and marine ecosystems, isotope pairing technology, intact core incubations

1 Introduction

The production of anthropogenic reactive nitrogen has intensified remarkably since the mid-20th century to meet the increasing global population (Kennedy, 2021). It is estimated that nitrogen is entering Earth's ecosystems at more than twice its natural rate, drastically disrupting the pristine nitrogen cycle (Canfield et al., 2010). Much of the excess nitrogen, primarily in the form of nitrate, is conveyed downriver to coastal and marine systems due to the low use efficiency of crops (Cui et al., 2013), resulting in a series of environmental issues including harmful algal blooms, eutrophication, and hypoxia (Dai et al., 2023). Consequently, it is critical to understand the transformations, particularly the fates of reactive nitrogen, encountering the fact that the nitrogen cycle has been intensively altered and is currently functioning beyond the safe operating space for humanity (Richardson et al., 2023).

Denitrification and anammox (Anaerobic Ammonium Oxidation) are two key nitrogen loss processes in aquatic environments, playing important roles in mitigating the adverse effects of excessive nitrogen inputs (Chen et al., 2021; Tan et al., 2022). Denitrification is the sequential reduction of nitrate, nitrite, nitric oxide, and nitrous oxide (N_2O) to dinitrogen gas (N_2), which is the most energetically favorable respiratory pathway in the absence of oxygen (Devol, 2015), serving as the predominant mechanism for nitrogen loss in coastal ecosystems (Damashek & Francis, 2018; Deng et al., 2024). Anaerobic ammonium oxidation (Anammox), an alternate nitrogen loss pathway, utilizes nitrite and ammonium to generate N_2 with no greenhouse gas N_2O production under anaerobic conditions (Graaf et al., 1995), and is a chemoautotrophic process with no direct demand for organic carbon (Strous et al., 1999). Therefore, anammox is an environment-friendly and energy-saving process compared to denitrification.

The ^{15}N isotope pairing technique (IPT) has been applied to a variety of sediments to quantify nitrogen loss rates in these settings (Nielsen, 1992; Robertson et al., 2019). Slurry incubation and intact core incubations in combination with IPT are two widely used methods for studying benthic nitrogen transformation pathways (Song et al., 2016b). Slurry incubations have been used to estimate the potential rates, and have advantages in discovering nitrogen loss processes in the environment (Thamdrup & Dalsgaard, 2002) as well as studying the environmental controls of these pathways, however, the natural gradients of substrates and redox in sediments were disrupted during incubations (Trimmer et al., 2006). The intact core incubations can quantify nitrogen removal processes in intact sediments and reflect the genuine benthic nitrogen transformation rates. The application of intact core incubations will enable us to fully clarify and understand the nitrogen cycle in field aquatic ecosystems.

Over the past thirty years, the introduction of isotope pairing technology has enabled numerous studies to measure anammox and denitrification using intact core incubations across a range of coastal and marine environments. These environments include intertidal wetlands (Adame et al., 2019; Liu et al., 2020), estuaries and coasts (Chen et al., 2021; Cheung et al., 2024; Deek et al., 2013; Hellemann et al., 2017), lagoons (Bernard et al., 2015; Magri et al., 2020) and oceans (Deutsch et al., 2010; Na et al., 2018). Despite decades of observations, the majority of studies on

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denitrification and anammox have been limited to local or regional scales. Various environmental factors, such as the availability of organic carbon (Yin et al., 2015) and nitrate (Asmala et al., 2017), dissolved oxygen (Bonaglia et al., 2013; Song et al., 2021), and temperature (Tan et al., 2022) influence these processes in coastal marine ecosystems. The modeling community also has conducted many researches on environmental regulation of nitrogen loss (mainly denitrification), and improved the predictive parameters of denitrification (Middelburg et al., 1996; Bohlen et al., 2012; Li et al., 2024). However, according to the currently available observational data, the global patterns and drivers of sediment nitrogen loss rates remain poorly understood in coastal and marine systems.

In view of the critical role of nitrogen removal processes and the current lack of a comprehensive database on actual nitrogen loss in coastal and marine systems, we have integrated actual nitrogen loss rates, including denitrification and anammox, from published studies, and constructed a dataset on nitrogen removal rates in these systems. This study provides a global-scale overview of the biogeography and potential controlling factors of denitrification and anammox in coastal and marine ecosystems. It also highlights the potential applications of this database such as using machine learning to predict the distribution of denitrification and anammox and offering a crucial dataset for the parameterization and development of biogeochemical models.

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2 Methods

2.1 Data compilation

Nitrogen loss rates, including denitrification and anammox measured through intact core incubations in coastal and marine ecosystems, were extracted from the literature published between 1996 and 2024. Table 1 summarized the locations, observation numbers, core incubation methods and references of nitrogen loss rates measurements. The intact core incubations in this study include both traditional core incubations (Bonaglia et al., 2017; Cheung et al., 2024) and continuous-flow experiments (Liu et al., 2020; McTigue et al., 2016). For continuous-flow experiments, incubations were carried out in a flow-through system where bottom water was pumped over intact cores using a multi-channel peristaltic pump, and inflow and outflow samples were collected to quantify the nitrogen process rates after the addition of ^{15}N tracer (Gardner & McCarthy, 2009). The peer-reviewed articles compiled in this study were sourced from the Web of Science database as of June 2024. The search terms were “denitrification” or “anammox” or “nitrogen loss” or “nitrogen removal”. Given a recent study has already summarized the data on nitrogen loss rates by slurry incubations in aquatic systems (He et al., 2025), this work only selected data in which denitrification and/or anammox rates were measured using intact core incubations with ^{15}N isotope pairing techniques, excluding measurements derived from slurry incubations. The intact core incubation experiments were primarily conducted in dark conditions and near-*in situ* or *in situ* ambient temperatures. Photosynthetic O_2

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production can influence O_2 penetration depth and thereby nitrate availability in sediments, interfering with denitrification rates in the nitrate reduction zone (Chen et al., 2021; Bartoli et al., 2021). In cases where nitrogen loss rates were measured under both light and dark conditions, only those measured in the dark were included to avoid photosynthesis and facilitate comparison with other studies. Measurements under light conditions have been detailed in studies reported by Bartoli et al. (2021), Chen et al. (2021), Risgaard-Petersen et al. (2004), Rysgaard et al. (1996b), and Welsh et al. (2000). Some studies have investigated the changes in nitrogen loss processes under varying oxygen concentrations (Bonaglia et al., 2013; Neubacher et al., 2011; Song et al., 2021), however, only nitrogen loss rates measured under ambient oxygen concentrations were extracted for this database. Some coastal zones are inhabited by plants and animals, whole core incubation would exclude the effect of benthic fauna or bioturbation as the nutrient and oxygen availabilities in the core might not reflect *in situ* sediment characteristics. In addition, whole core incubation would exclude the effect of antibiotics addition because antibiotics addition could influence *in situ* nitrogen removal rates (Wan et al., 2023). Thus, studies examining the effects of meiofauna or antibiotics on nitrogen removal were not included (Bonaglia et al., 2014b; Wan et al., 2023), only rates measured without meiofauna or antibiotic additions were considered. At least one environmental variable was recorded for each selected study, and means and sample sizes had to be reported for nitrogen removal rates. Articles that only reported nitrogen loss rates without any environmental variables were excluded. Data on total nitrogen loss rates (the sum of denitrification

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and anammox), denitrification rates, anammox rates, and related environmental variables were collected from tables, text, and/or supplementary materials, and in some cases, extracted from graphs using Origin 2020 software. The unit conversions were performed where necessary. For example, nitrogen loss (including denitrification and anammox) rates were in μmol N m^{-2} h^{-1}. When rates in the texts were displayed as mmol N m^{-2} d^{-1} or μmol N m^{-2} d^{-1}, they were converted to μmol N m^{-2} h^{-1}. In addition, longitude and latitude were extracted from figures from published articles if not shown in the main text.

The database includes observation details (year of sampling, month of sampling, latitude, and longitude), sediment parameters, and water physicochemical factors, such as sediment organic carbon, the ratios of carbon to nitrogen (C/N ratios), oxygen penetration depth, and water salinity, depth, temperature, DO, ammonium and nitrate concentrations. Note that some environmental variables were not reported in the original studies. NM represents parameters that were not measured, and empty or NA indicates data not available or reported. In total, the database comprises 473, 466, 255, and 255 measurements of total nitrogen loss rates, denitrification rates, anammox rates, and the relative contribution of anammox to total nitrogen loss, respectively. Authors and interested readers are welcomed to contact us to indicate an error or update the data in the database.

For quality control, extreme nitrogen loss rate values were excluded from the database following Chauvenet's criterion (Glover et al., 2011), a method typically applied to normally distributed data to identify outliers whose deviation from the mean has a probability lower than 1/(2n). More details about Chauvenet's criterion can be found in Glover et al., (2011) and Buitenhuis et al. (2013). Very high rates of denitrification were observed in the Tama Estuary, Japan (Usui et al., 2001), a constructed wetland in Casino, NSW, Australia (Erler et al., 2008), a coastal lagoon in Sacca di Goro lagoon, Italy (Magri et al., 2020) and the Tropical Coastal Wetlands, Australia (Adame et al., 2019). For anammox, high rates were found only in a constructed wetland in Casino, NSW, Australia (Erler et al., 2008). Similarly, high values for anammox's contribution to total nitrogen loss were observed in the Changjiang River Estuary (also called Yangtze River Estuary), China (Liu et al., 2020), the Norwegian Trench, Skagerrak (Trimmer et al., 2013), and the Great Barrier Reef lagoon (Erler et al., 2013), with contributions exceeding 70%. Observations with nitrogen loss rates of 0 or NA were excluded from the outlier analysis. For example, anammox rates of 0 were reported in the Changjiang River Estuary, China (Liu et al., 2020), the North Sea (Neubacher et al., 2011; Rosales Villa et al., 2019), the Pearl River Estuary, China (Tan et al., 2019), the Norwegian Trench, Skagerrak (Trimmer et al., 2013), and the Gulf of Finland, Baltic Sea (Jäntti et al., 2011). After excluding observations of 0 and NA (0, 8, 252, and 253 observations for total nitrogen loss rates, denitrification rates, anammox rates, and anammox's contribution to total nitrogen loss), the nitrogen loss rates were natural-log transformed for further analysis.

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2.2 Methods for measuring denitrification and anammox rates

Before the discovery of anammox, denitrification was regarded as the sole significant pathway responsible for nitrogen loss (Dalsgaard & Thamdrup, 2002). The ^{15}N isotope pairing technique (IPT) was developed to quantify denitrification rates (Nielsen, 1992). In this method, the overlying water of intact sediment cores is enriched with $^{15}NO_3^-$, which is mixed with the naturally occurring $^{14}NO_3^-$. After a few hours of incubation, the denitrification products, ^{15}N-labeled dinitrogen gas ($^{29}N_2$ and $^{30}N_2$), are measured. Incubations to measure nitrogen loss rares have been mostly conducted in dark conditions and near-*in situ* or *in situ* ambient temperatures. After incubating for 1 h to over 96 h, the incubation is halted by injecting saturated $HgCl_2$ or $ZnCl_2$ saturation solution or 37% formaldehyde. The samples are then preserved for $^{15}N_2$ gas analyses through isotope ratio mass spectrometer (IRMS) or membrane inlet mass spectrometry (MIMS). Key experimental details, such as incubation conditions, temperature control, incubation time, termination, and calculation references, are compiled in the database if provided in the original studies. For more detailed experimental information, refer to the corresponding references.

The production rate of unlabeled $^{14}NO_3^-$ (IPT*p*14, also referred to as the genuine production of N_2) can be calculated based on the assumption of random isotope pairing during the denitrification of the uniformly mixed NO_3^- species. The following equation is commonly used to estimate the genuine N_2 production (Nielsen, 1992; Steingruber et al., 2001).

$$\mathrm{IPT}p14 = \frac{p^{29}\mathrm{N}_2}{2\times p^{30}\mathrm{N}_2}\times(p^{29}\mathrm{N}_2 + 2\times p^{30}\mathrm{N}_2) \quad (1)$$

Where $p^{29}N_2$ and $p^{30}N_2$ represent the total production rates of $^{29}N_2$ and $p^{30}N_2$, respectively.

Thamdrup and Dalsgaard (2002) were the first to quantify anammox through anaerobic slurry incubations in natural environments, discovering that anammox could account for more than 60% of total N_2 production. This highlighted the significant role of anammox in nitrogen removal. Following this, Risgaard-Petersen et al. (2003) proposed a modification to the traditional IPT, allowing for more accurate quantification of true N_2 production in environments where anammox and denitrification coexist. This revision also enables the distinction between N2 produced by anammox and denitrification. The revised IPT (rIPT) follows the same procedure as the classical IPT, with $^{15}NO_3^-$ added to the overlying water of intact sediment cores, though the calculation process is more complex. The following equations are commonly used to estimate the actual N_2 production (rIPTp14) and denitrification (p14DEN) as well as anammox (p14ANA) (Risgaard-Petersen et al., 2003; Trimmer & Nicholls, 2009; Trimmer et al., 2006). The total N_2 production rate is the sum of denitrification and anammox rates.

$$\mathrm{rIPT}p14 = 2r_{14}\times(p^{29}N_2 + p^{30}\mathrm{N}_2\times(1-r_{14})) \quad (2)$$

$$p14\mathrm{DEN} = 2r_{14}\times(r_{14}+1)\times p^{30}\mathrm{N}_2 \quad (3)$$

$$p14\mathrm{ANA} = 2r_{14}\times(p^{29}\mathrm{N}_2 - 2\times r_{14}\times p^{30}\mathrm{N}_2) \quad (4)$$

In these equations, $p^{29}N_2$ and $p^{30}N_2$ are the total production rates of $^{29}N_2$ and $p^{30}N_2$, respectively, and r_{14} represents the ratio of $^{14}NO_3^-$ and $^{15}NO_3^-$ in the nitrate reduction zone. There are 3 different methods to estimate r_{14}, with detailed explanations available in Trimmer et al. (2006).

Subsequently, Hsu and Kao (2013) revised the rIPT method to incorporate both N_2O production and anammox, enabling the determination of the absolute rate of each nitrogen loss pathway, including denitrification, anammox, and N_2O production from denitrification. Denitrification and anammox measurements based on the method of Hsu and Kao (2013) are included in this database, whereas data on the true N_2O production rate have not been included.

Regarding the aforementioned calculation methods, Salk et al. (2017) have systematically reviewed different methods for quantifying nitrogen loss rates and illustrated their differences with diagrams distinguishing different processes, providing valuable guidance for researchers interested in this field. Therefore, interested researchers can refer to their article.

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3 Results and discussion

3.1 Overview of the database

Overall, there are 473, 466, and 255 measurements for total nitrogen loss denitrification and anammox, respectively (Fig. 1). Denitrification and anammox have been measured simultaneously at 255 observations. The observations of nitrogen loss rates are primarily distributed in the Eastern coast of the United States, the Baltic Sea, the Eastern Coast of China, the Eastern Coast of Australia, and polar regions of the Northern Hemisphere (Fig. 1a). Before 2000, nitrogen loss measurements were predominantly focused on denitrification, while both denitrification and anammox rates have been measured concurrently since 2000 (Fig. 1b). Notably, more observations were recorded in 2011 and 2017. The studies in 2011 were mainly conducted in the Changjiang estuary and its adjacent East China Sea (Song et al., 2021), the Jinpu Bay, China (Yin et al., 2015), the North Sea (Bale et al., 2014), the Northern Baltic Proper (Bonaglia et al., 2014a) and the hypoxic zone off the Changjiang River estuary, China (Yang et al., 2022). In 2017, high observations were found in the Northern East China Sea, China (Chang et al., 2021), the Changjiang River Estuary, China (Liu et al., 2020; Liu et al., 2019; Tan et al., 2022), the Coast of Victoria, Australia (Kessler et al., 2018) and the Jiulong River Estuary, China (Tan et al., 2022).

3.2 Distribution of denitrification

In total, the vast majority of nitrogen loss rate measurements were conducted in the Northern Hemisphere, and data in the Southern Hemisphere were limited (Fig. 2a, 2b, 2c). The low and middle latitudes of the Northern Hemisphere have a large body of observations, especially in the 20-30°N, 30-40°N, and 50-60°N latitude bands. Denitrification rates ranged from 0.04 to 750 μmol N m^{-2} h^{-1}, with a median value of 7.72±4.30 μmol N m^{-2} h^{-1}. There is a decreasing trend in the denitrification rates with latitude in the Northern Hemisphere, though the observations in the high latitude are still limited. The measurements of denitrification were primarily conducted between

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April and September (Fig. 2d, 2e, 2f). On a global scale, no clear seasonal pattern for denitrification rates was observed.

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3.3 Distribution of anammox

From a latitude perspective, the distribution of anammox rates closely mirrored that of denitrification, with the majority of observations concentrated in the 20-30°N, 30-40°N, and 50-60°N latitude bands (Fig. 3a, 3b, 3c). However, compared to denitrification, there were fewer anammox observations. Anammox rates spanned from 0.01 to 48.94 μmol N m^{-2} h^{-1}, with a median value of 1.00±0.39 μmol N m^{-2} h^{-1}. Similar to denitrification, anammox rates also showed a decreasing trend with increasing latitude in the Northern Hemisphere. Numerous anammox measurements were conducted between April and September, consistent with the timing of denitrification measurements (Fig. 3d, 3e, 3f). Additionally, February saw a high number of anammox observations, and these observations were predominantly conducted at the north East China Sea (Chang et al., 2021), the Changjiang Estuary (Liu et al., 2019) and the Northeastern New Zealand continental shelf regions (Cheung et al., 2024). On a global scale, there was no clear seasonal pattern for anammox rates.

3.4 Distribution of contribution of anammox to total N_2 production

The relative importance of anammox to total N_2 production increased first and then decreased, peaking in the 40-50°N latitudinal band in the Northern Hemisphere, although data points in this band were limited (Fig. 4). The contribution of anammox to total N_2 production varied from 0.22% to 67.33%, with a median value of 12.29%. The highest value (67.33%) was recorded at a site on the North Atlantic continental slope at a depth of 2000 m (Trimmer & Nicholls, 2009), where anammox accounted for the majority of nitrogen removal. There were no significant monthly changes in the relative importance of anammox to total nitrogen loss, except for March, when anammox contributed a notably high percentage. High values in March were observed in the Ulleung Basin, East Sea, and the continental shelf and slope, North Atlantic (Na et al., 2018; Trimmer & Nicholls, 2009) where the stations were characterized by low nitrate levels or deep water. These environmental conditions may inhibit denitrification, thereby increasing the relative contribution of anammox to nitrogen loss. It is worth noting that the rate observations in March were mainly distributed in certain regions. Thus, the extrapolations of relative importance of anammox in coastal marine ecosystems at the monthly level using this result should be cautious. More observation data in other regions are needed in the future.

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3.5 Control factors on denitrification and anammox rates

The variations in denitrification rates and anammox rates were compared against several environmental variables, including sediment organic carbon, the ratios of carbon to nitrogen (C/N ratios) and oxygen penetration depth, and water depth, temperature, salinity, dissolved oxygen, ammonium, and nitrate concentrations. This comparison was conducted to evaluate the main controlling factors of nitrogen loss rates.

There was no significant relationship between denitrification rates and the contents of sediment organic carbon (p>0.05; Fig. 5a). Heterotrophic denitrification is primarily carried out by facultative anaerobic heterotrophs (Devol, 2015), which use organic carbon as an electron donor and energy source. Therefore, higher organic carbon levels might be expected to promote denitrification (Damashek & Francis, 2018). However, no such relationship was observed in this dataset. Denitrification rates increased with sediment carbon nitrogen ratios (r=0.32, p<0.01; Fig. 5b). The C/N ratios can indicate the reactivity of sediment organic material, with lower C/N values generally representing more reactive organic matter (Cheung et al., 2024; Erler et al., 2013). Typically, high denitrification rates are associated with sediments that have lower C/N ratios. However, in this analysis, the opposite trend was observed. One possible explanation is that microbial communities may adapt to use organic matter typically encountered, though the organic matter is not labile (Salk et al., 2017). Denitrification rates showed a weak negative correlation with oxygen penetration depth (r=-0.29, p<0.01; Fig. 5c), as greater O_2 penetration may be adverse to the

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occurrence of denitrification (Cheung et al., 2024). Denitrification rates also decreased with water depth (r=-0.26, p<0.01; Fig. 5d), with most observations occurring at depths shallower than 250 m. Denitrification was positively correlated with higher water temperatures (r=0.38, p<0.01; Fig. 5e), and negatively correlated with salinity (r=-0.15, p<0.01; Fig. 5f), with most rates falling within two salinity ranges (0-10 and 30-40). Samples that had a salinity greater than 40 were collected in hypersaline lagoons of tropical regions (Enrich-Prast et al., 2016). The relationship between denitrification and salinity across coastal environments has been summarized by Torregrosa-Crespo et al. (2023) and will not be further elaborated here. There was a weak negative relationship between denitrification rates and dissolved oxygen concentrations (r=-0.23, p<0.01; Fig. 5g). Overall, higher denitrification rates were recorded in areas with high nitrate concentrations (r=0.16, p<0.01; Fig. 5h), suggesting the importance of nitrate substrate in regulating denitrification, though some high rates were also observed in sites with low nitrate levels. No significant correlation was found between denitrification rates and ammonium concentrations (p>0.05; Fig. 5i).

Anammox rates showed a weak positive correlation with sediment organic carbon (r=0.16, p<0.05; Fig. 6a). Although anammox is an autotrophic process that does not require organic carbon as an electron donor (Salk et al., 2017), some studies have reported links between sediment organic carbon content and anammox rates. For example, studies in subtropical mangrove sediments (Meyer et al., 2005) and the

Thames estuary (Trimmer et al., 2003) found that higher organic matter stimulated anammox. This correlation may be due to enhanced mineralization leading to increased ammonium production, which indirectly stimulates anammox (Damashek & Francis, 2018), as sediment organic carbon can serve as a proxy for organic carbon mineralization (Song et al., 2016a). Similar to denitrification, high anammox rates were observed at sites with elevated C/N ratios (r=0.33, p<0.01; Fig. 6b). We infer that, to some extent, the coupling of denitrification and anammox may account for this relation. As mentioned above, denitrification stimulated with higher C/N ratios, decomposition of organic matter could provide substrate for anammox, thereby promoting anammox. More studies are needed to reveal the influencing mechanisms of C/N ratios on anammox. No clear trend was found between anammox rates and oxygen penetration depth (p>0.05; Fig. 6c), and high anammox rates were observed in shallow waters (p>0.05; Fig. 6d). Anammox rates showed a weak positive correlation with temperature (r=0.19, p<0.01; Fig. 6e). While several studies have suggested that low temperatures could favor anammox (Dalsgaard & Thamdrup, 2002; Rysgaard et al., 2004; Tan et al., 2020), these studies primarily measured anammox potential using anaerobic slurry incubations. Contrary to previous findings, our study showed that actual anammox rates increased with rising temperatures, suggesting a discrepancy between the effects of temperature on actual and potential anammox rates. Future research is needed to investigate the underlying mechanisms for these inconsistent results. Anammox rates decreased with increasing salinity (r=-0.38, p<0.01; Fig. 6f), and showed no significant relationship with dissolved oxygen (p>0.05; Fig. 6g). A

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删除[小子]: organic matter quantity and quality weak positive correlation was observed between anammox rates and nitrate concentration (r=0.41, p<0.01; Fig. 6h), highlighting the importance of substrates in regulating anammox. Although anammox uses nitrite as an electron acceptor rather than nitrate (Graaf et al., 1995), nitrate reduction can produce nitrite, which promotes anammox activity. No relationship was found between anammox rates and ammonium concentration (p>0.05; Fig. 6i).

Through the correlation analysis of global-scale compiled data, we identified that sediment C/N ratios, oxygen penetration depth, water depth, temperature, salinity, dissolved oxygen, and nitrate concentrations were the main factors regulating denitrification rates, whereas sediment organic carbon, C/N ratios, temperature, salinity, and nitrate concentrations primarily controlled anammox rates (Fig. 5 and Fig. 6).

Other factors, such as iron, manganese, and sulfide, although not included in the database, can also influence denitrification and anammox rates. For example, Fe oxides were observed to be positively correlated with denitrification rates in the Jinpu Bay, China (Yin et al., 2015). The mechanism may be that ferrous iron can supply an electron donor for nitrate, thereby promoting denitrification. Anschutz et al. (2000) found manganese dioxides could also serve as electron donors for denitrification. Deng et al. (2015) showed a positive relationship between denitrification rates and sulfide concentrations in the Changjiang Estuary sediments, revealing that sulfide can act as energy sources for denitrification. In contrast, evidence has shown that sulfide exerts inhibitory effects on nitrogen removal in coastal sediments by inhibiting the

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metabolism of denitrifying microorganisms (Aelion and Warttinger, 2010). Thus, the impact of sulfide on denitrification remains controversial. For anammox, a study found that sulfide could affect anammox activity. Yin et al. (2015) found that anammox rates were positively correlated with sulfide concentrations. This phenomenon is likely attributed to sulfide-induced nitrite accumulation during incomplete denitrification processes, where sulfide inhibits the activity of nitric oxide reductase and nitrous oxide reductase, thereby enhancing anammox activity. Under anaerobic conditions, ammonium oxidation can be coupled with the reduction of ferric iron, sulfate, and Mn(IV)-oxides. For example, Rios-Del Toro et al. (2018) confirmed that ammonium oxidation was associated with ferric iron and sulfate reduction under anaerobic conditions, thereby stimulating nitrogen loss in marine sediments. Evidence shows ammonium loss is coupled with Fe(III) and Mn(IV) reduction in coastal environments (Samperio-Ramos et al., 2024), demonstrating the crucial roles of metal oxides in removing reactive nitrogen.

Liu et al. (2020) have examined the spatio-temporal changes of *in situ* nitrogen loss processes in intertidal wetlands of the Yangtze Estuary and found that denitrification was linked to anammox, implying the coupling of denitrification and anammox on a local scale. Consistent with their findings, this work also found denitrification was positively correlated to anammox (r=0.67, p<0.01; Fig. 7). A majority of denitrifying bacteria are heterotrophic and the decomposition of organic matter is accompanied by the production of ammonium (Devol, 2015), supplying substrates for anammox. Thus,

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3.6 Drivers on contribution of anammox to total nitrogen loss

We made simple correlation analysis between the contribution of anammox to total N_2 production (ra) and environmental parameters (Fig. 8). There was a positive correlation between ra and water depth (r=0.59, p<0.01; Fig. 8d). Similar findings were found on the Northeastern New Zealand continental shelf (Cheung et al., 2024) and the continental shelf and slope, North Atlantic (Trimmer & Nicholls, 2009). The increased importance of anammox can be attributed to the significant attenuation of denitrification with depth, as the availability of organic carbon essential for heterotrophic denitrification generally decreases with water depth (Thamdrup, 2012). In addition to water depth, other factors such as oxygen penetration depth, C/N ratios, and temperature may also influence the relative importance of anammox. The ra was positively correlated with oxygen penetration depth (r=0.7, p<0.01; Fig. 8c). As previously mentioned, denitrification decreases with higher oxygen penetration depth, likely increasing the relative importance of anammox indirectly. Conversely, ra showed a decreasing trend with elevated C/N ratios (r=-0.35, p<0.01; Fig. 8b). High C/N ratios may promote denitrification more significantly than anammox because both processes tend to enhance with increasing C/N ratios, leading to a decrease in the relative importance of anammox at sites with high C/N ratios. Additionally, ra was

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negatively correlated with temperature (*r*=-0.29, $p<0.01$; Fig. 8e), indicating that denitrification is stimulated at higher temperatures compared to anammox. Temperature-controlled experiments have confirmed that denitrification has a greater optimal temperature than anammox (Canion et al., 2014; Tan et al., 2020). No correlations were found between ra and other environmental factors, including sediment organic carbon, water salinity, dissolved oxygen, nitrate, and ammonium concentrations. (all $p>0.05$; Fig. 8a, 8f, 8g, 8h, 8i). Based on the simple correlation analysis of global-scale compiled data, we identified that sediment C/N ratios, oxygen penetration depth, water depth and temperature were the primary factors governing the relative contribution of anammox to total nitrogen loss (Fig. 8).

4 Applications of the database

This database serves as a valuable resource for the broad scientific communities that are interested in nitrogen cycle processes within coastal and marine ecosystems, particularly those focusing on denitrification and anammox. The data is made accessible as a basic database that will lead to a deeper understanding and generate new scientific insights into the nitrogen cycles at the global scale. Potential applications of this database include: (1) serving as a reference for comparing denitrification and anammox rates across different spatial scales including local, regional, and global scales or across different habitats such as coastal wetland, estuary, lagoon, and ocean in future studies, (2) identifying and comparing the controlling

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factors of denitrification and anammox at various spatial scales. Note that environmental variables have missing values, which limits our analysis of environmental factors affecting nitrogen loss rates. For better studying the environmental controlls, these missing values can be filled using the multivariate imputation with random forests method (Hou et al., 2021). (3) predicting the global biogeography of denitrification and anammox in coastal and marine systems through machine learning methods. For example, by integrating potential key factors of nitrogen removal processes into machine learning architectures, future studies can develop spatially predictive models for global nitrogen loss rates by the references of Laffitte et al. (2025) and Ling et al. (2025). (4) providing essential data for the parameterization, validation and enhancement of Earth system biogeochemical models. The previous model considered constraint parameters such as nitrate, dissolved oxygen, chlorophyll, and phosphate content (Middelburg et al., 1996; Bohlen et al., 2012; Li et al., 2024), and other parameters provided in this dataset can supply new parameter supplements for the development of biogeochemical model. (5) guiding future observations. More studies are needed in areas and months with limited observation data on nitrogen loss rates to deepen our understanding of the nitrogen cycle worldwide. Additionally, when studying nitrogen loss rates, particular attention should be paid to enhancing the monitoring of multiple environmental parameters.

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5 Conclusions

We compiled and presented a global database of denitrification and anammox measurements obtained from core incubation experiments in coastal and marine sediments. To our knowledge, no efforts have been made to compile actual nitrogen loss rates and associated environmental factors in coastal and marine regions on a global scale. This database offers valuable insights into the spatiotemporal variations and potential controlling factors of denitrification and anammox, along with the contribution of anammox to total N_2 production. The establishment of this global database on denitrification and anammox in coastal and marine sediments provides a critical foundation for advancing nitrogen cycle research and generating novel insights. This database enables the comparison of these two nitrogen loss processes, evaluation of the environmental controls across spatial scales (local to global), prediction of the global biogeography of denitrification and anammox, parameterization and development of biogeochemical models, and guide direction of observations in the future.

Data availability

The data used in this study are openly available in Figshare repository at https://doi.org/10.6084/m9.figshare.27745770.v3 (Chang et al., 2024).

Author contributions

SJK and EHT conceived the research. YKC and EHT compiled the data. YKC, EHT,

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DZG, CL and SJK participated in the data analysis. All co-authors contributed to the writing and reviewing of this manuscript.

Competing interests

None declared.

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Figures and Table

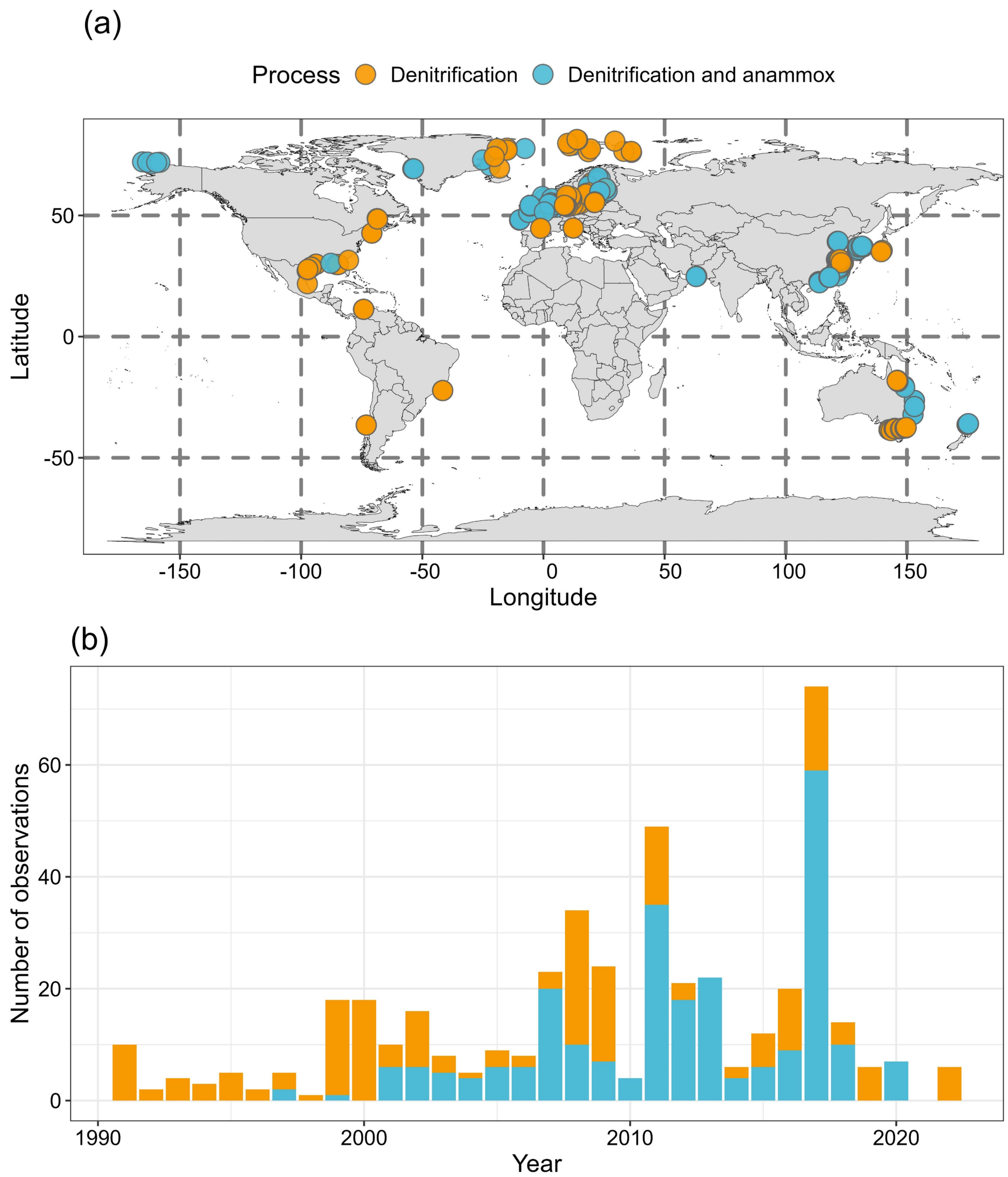

Figure 1 Map showing the sampling sites distribution of nitrogen loss rate measurements (a) and the number of rate observations each year (b). Orange solid points denote that only denitrification rates were measured. Cyan solid points denote that both denitrification and anammox rates were measured.

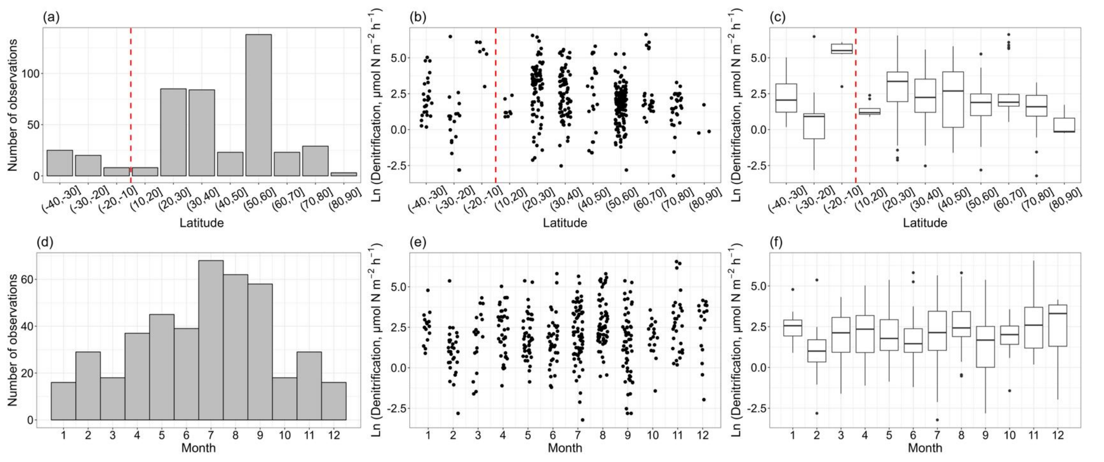

Figure 2 The observation numbers of denitrification (a, d) and denitrification rates (b, c, e, f) with latitudinal bands and months. A vertical dashed red line delimits the Southern Hemisphere and the Northern Hemisphere. The box plots show the median, interquartile range, and outliers for each latitudinal band and month.

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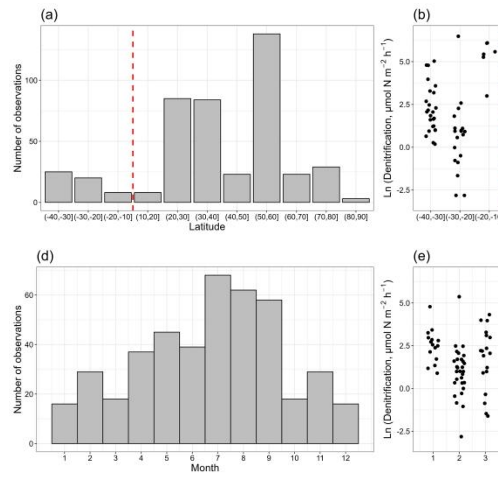

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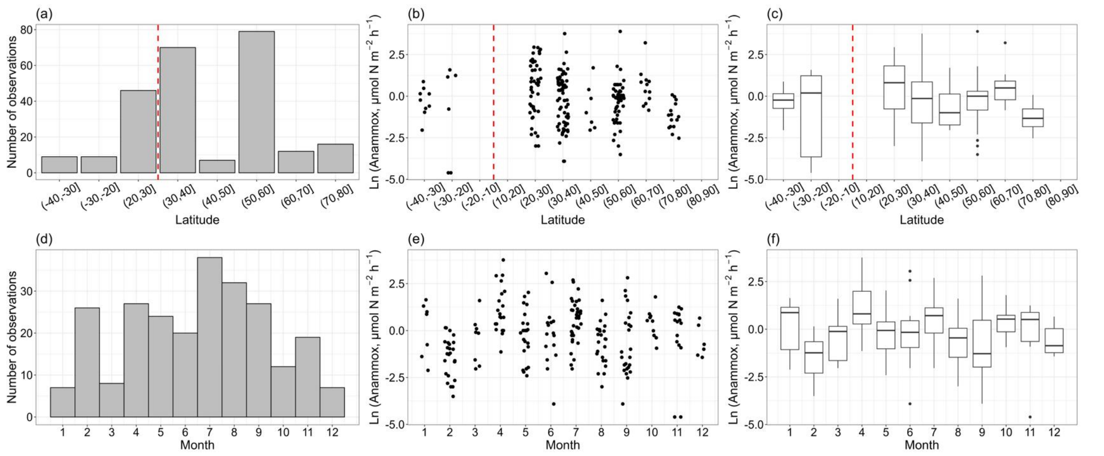

Figure 3 The observation numbers of anammox (a, d) and anammox rates (b, c, e, f) with latitudinal bands and months.

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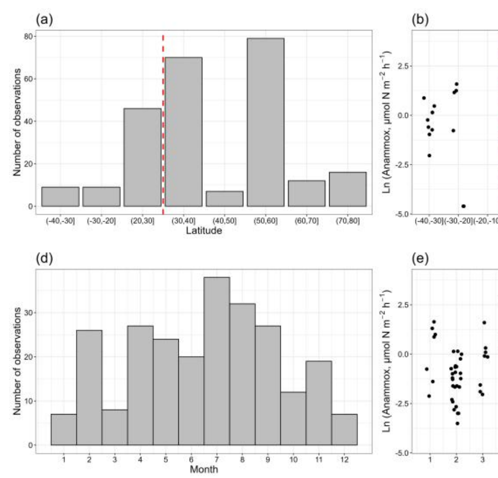

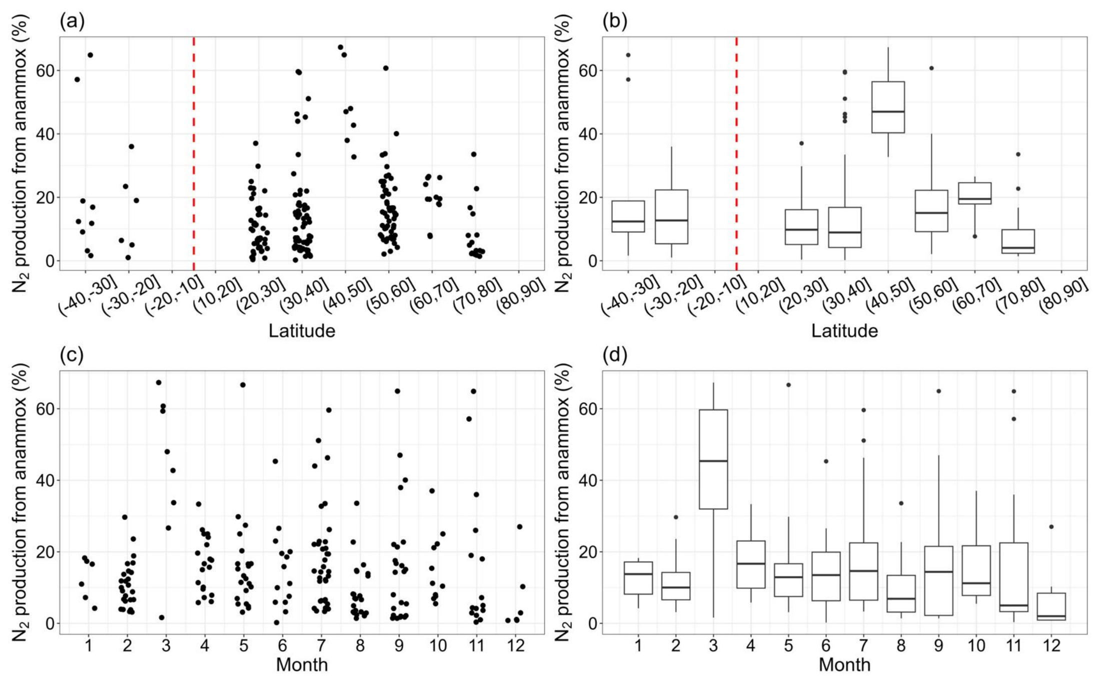

Figure 4 The contribution of anammox to total N_2 production with latitudinal bands (a, b) and months (c, d).

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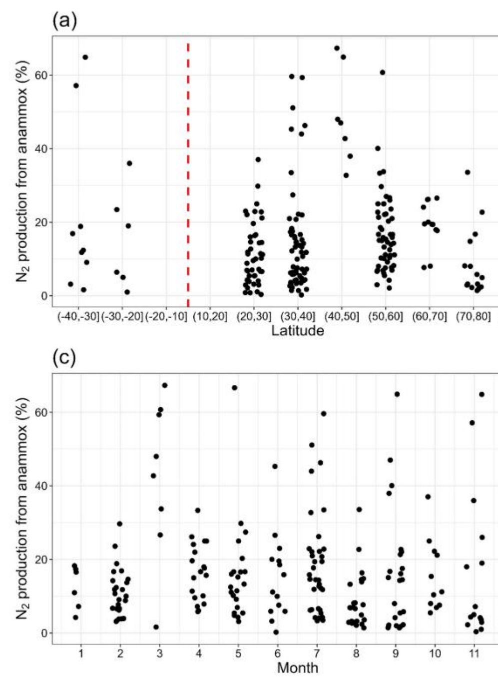

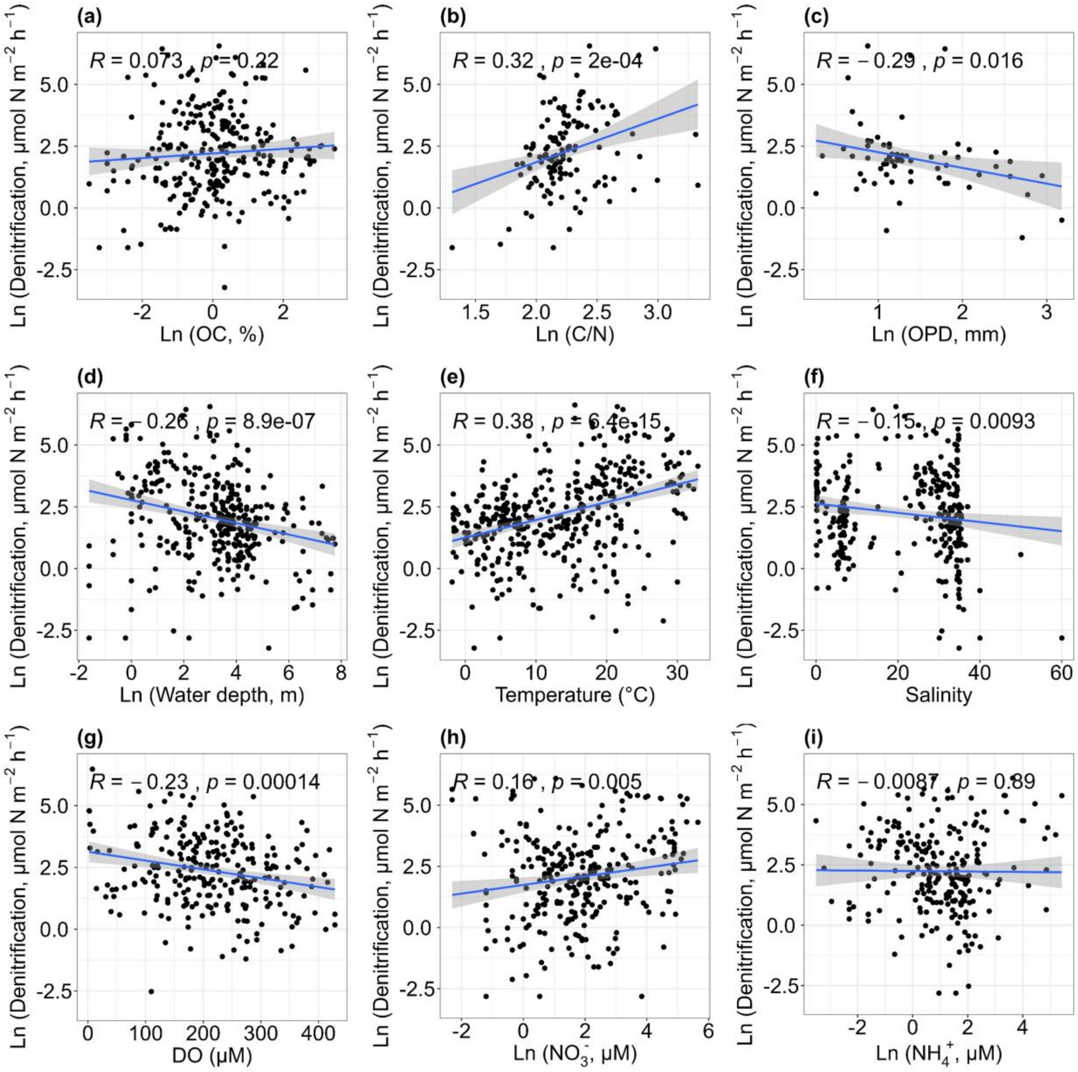

Figure 5 Relationships between denitrification rates and organic carbon [OC, (a)], carbon-nitrogen ratios [C/N, (b)], oxygen penetration depth [OPD, (c)], water depth (d), temperature (e), salinity (f), dissolved oxygen [DO, (g)], nitrate concentrations [NO_3^-, (h)] and ammonium concentrations [NH_4^+, (i)].

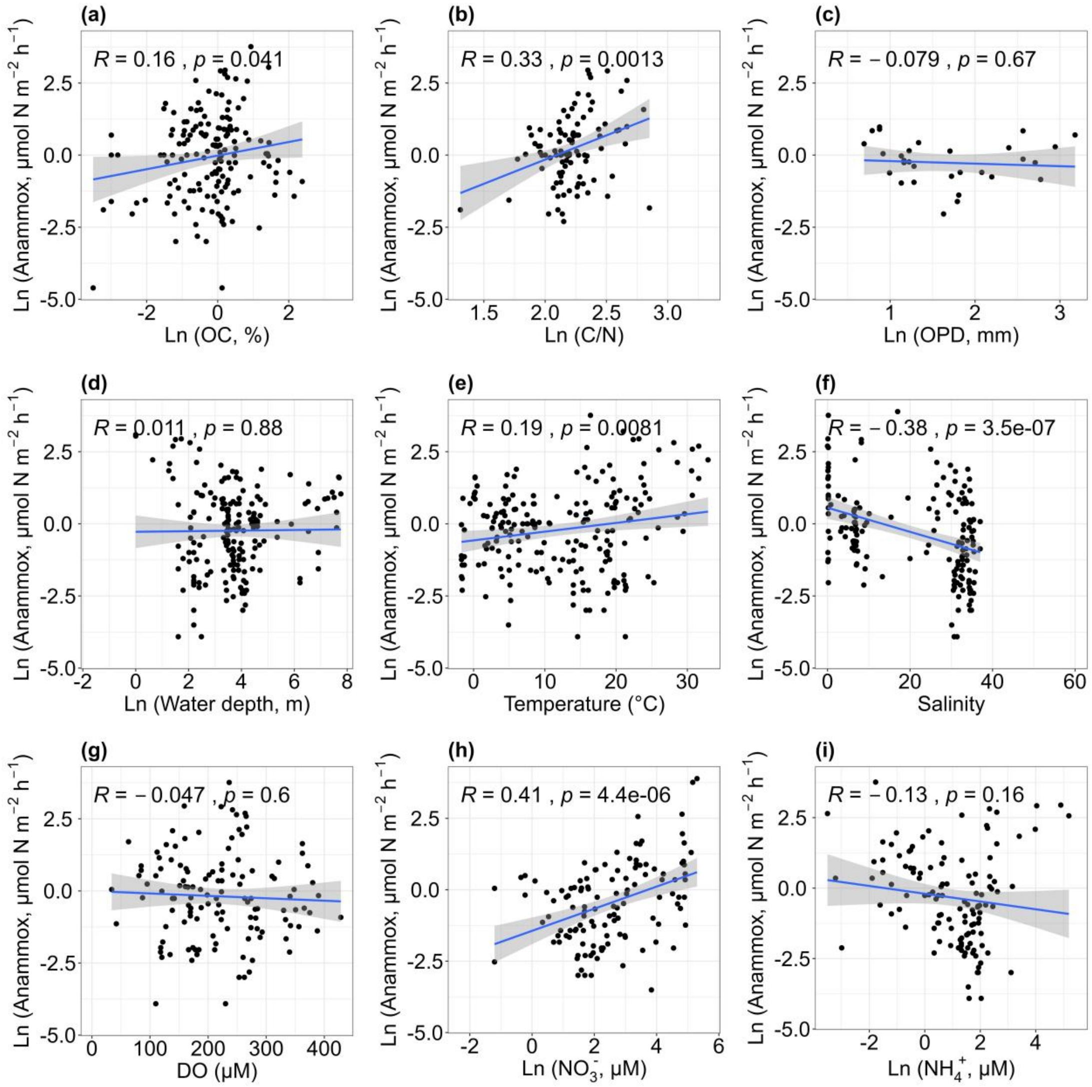

Figure 6 Relationships between anammox rates and organic carbon [OC, (a)], carbon-nitrogen ratios [C/N, (b)], oxygen penetration depth [OPD, (c)], water depth (d), temperature (e), salinity (f), dissolved oxygen [DO, (g)], nitrate concentrations [NO_3^-, (h)] and ammonium concentrations [NH_4^+, (i)].

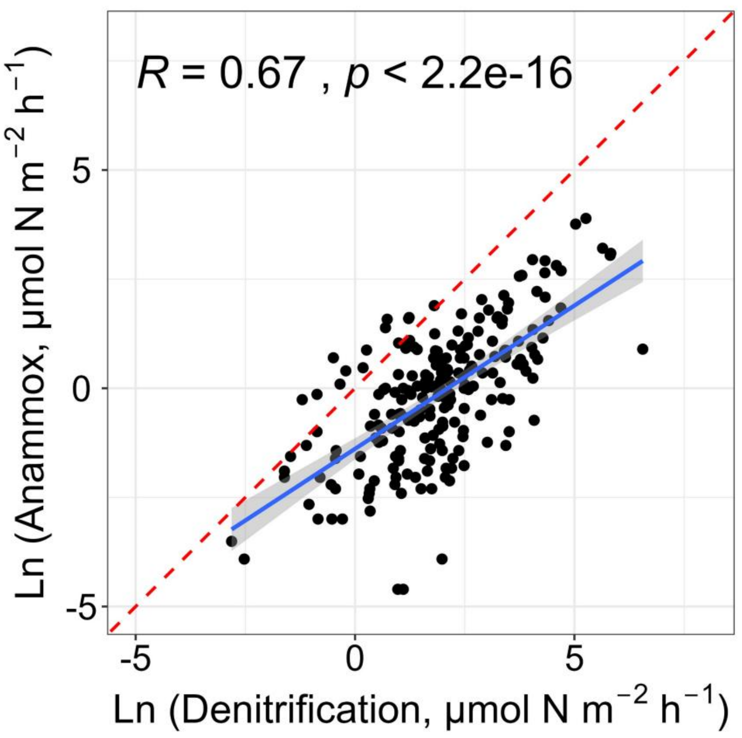

Figure 7 Relationships between denitrification and anammox rates. The blue solid line and red dashed line denote the linear regression and 1:1 line, respectively.

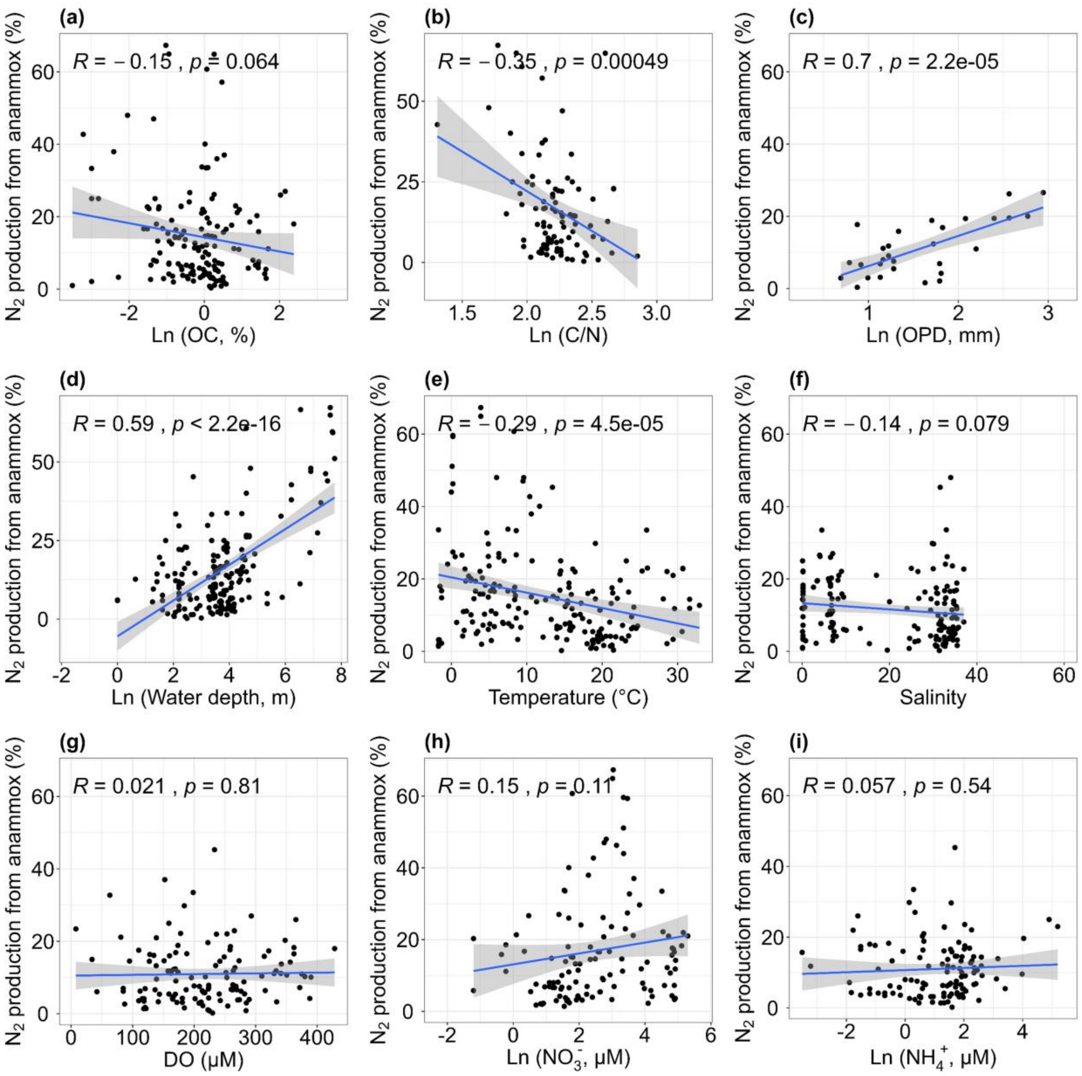

Figure 8 Relationships between the relative contribution of anammox to total N_2 production and organic carbon [OC, (a)], carbon-nitrogen ratios [C/N, (b)], oxygen penetration depth [OPD, (c)], water depth (d), temperature (e), salinity (f), dissolved oxygen [DO, (g)], nitrate concentrations [NO_3^-, (h)] and ammonium concentrations [NH_4^+, (i)].

Table 1 Summary of the observations of actual nitrogen loss rates. The locations, water depth range, observation numbers, core incubation methods and references are listed.

Sampling locations	Water depth (m)	Observation numbers	Core incubations	References
Aarhus Bright, Denmark	16	2	Intact core incubations	(Nielsen and Glud, 1996)
Arabian Sea	360 - 1430	4	Intact core incubations	(Sokoll et al., 2012)
Arctic fjord (Svalbard, Norway)	51 - 211	3	Intact core incubations	(Gihring et al., 2010b)
Bassin d'Arcachon coastal lagoon	NM	3	Intact core incubations	(Welsh et al., 2000)
Casino, NSW, Australia	NM	2	Intact core incubations	(Erler et al., 2008)
central Sagami Bay, Japan	25.1 - 59	1	Intact core incubations	(Glud et al., 2009)
Changjiang estuary and its adjacent East China Sea	1.9 - 58	7	Intact core incubations	(Song et al., 2021)
Changjiang River Estuary and Jiulong River Estuary, China	NM	23	Intact core incubations	(Tan et al., 2022)
Changjiang River Estuary, China	6 - 61	22	Continuous-flow experiments	(Liu et al., 2020)
Changjiang River Estuary, China	24 - 33	14	Continuous-flow experiments	(Liu et al., 2019)
Coast of Finland, northern Baltic Sea	1.5 - 8	10	Intact core incubations	(Hellemann et al., 2020)
Coast of Victoria, Australia	5 - 24	11	Intact core incubations	(Kessler et al., 2018)
Coastal area of the Gulf of Gdańsk	NM	6	Intact core incubations	(Benelli et al., 2024)
Coastal lagoons, France	36 - 100	6	Intact core incubations	(Rysgaard et al., 1996b)
Coastal sediments, Greenland	50 - 2000	11	Intact core incubations	(Rysgaard et al., 2004)
Continental shelf and slope, North Atlantic	85	12	Intact core incubations	(Trimmer and Nicholls, 2009)
Continental shelf region off central Chile	NM	5	Intact core incubations	(Farías et al., 2004)
Danshuei River in northern	19 - 43.5	1	Intact core	(Hsu and Kao,

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Observation numbers
Core incubations
References

Aarhus Bright, Denmark
2
Intact core incubations
(Nielsen and Glud, 1996)

Arabian Sea
4
Intact core incubations
(Sokoll et al., 2012)

Arctic fjord (Svalbard, Norway)
3
Intact core incubations
(Gihring et al., 2010b)

Bassin d'Arcachon coastal lagoon
3
Intact core incubations
(Welsh et al., 2000)

Casino, NSW, Australia
2
Intact core incubations
(Erler et al., 2008)

central Sagami Bay, Japan
1
Intact core incubations
(Glud et al., 2009)

Changjiang estuary and its adjacent East China Sea
7
Intact core incubations
(Song et al., 2021)

Changjiang River Estuary and Jiulong River Estuary, China
23
Intact core incubations
(Tan et al., 2022)

Changjiang River Estuary, China
22
Continuous-flow experiments
(Liu et al., 2020)

Changjiang River Estuary, China
14
Continuous-flow experiments

Taiwan, China			incubations	2013)
East China Sea	0.7 - 7.9	2	Intact core incubations	(Song et al., 2016)
Elbe Estuary, North Frisian Wadden Sea	115 - 329	5	Intact core incubations	(Deek et al., 2013)
Fjords in Svalbard and northern Norway	27 - 40	5	Intact core incubations	(Glud et al., 1998)
Georgia continental shelf, USA	5 - 29	2	Intact core incubations	(Vance-Harris and Ingall, 2005)
Great Barrier Reef lagoon	12.5 - 111	2	Intact core incubations	(Erler et al., 2013)
Gulf of Bothnia, Baltic Sea	13 - 85	7	Intact core incubations	(Bonaglia et al., 2017)
Gulf of Finland	58 - 83	5	Intact core incubations	(Susanna, 2007)
Gulf of Finland, Baltic Sea	NM	11	Intact core incubations	(Jäntti and Hietanen, 2012)
Gulf of Finland, Baltic Sea	33	13	Intact core incubations	(Jäntti et al., 2011)
Gulf of Finland, Baltic Sea	NM	5	Intact core incubations	(Hietanen and Kuparinen, 2008)
Gulf of Mexico	116	6	Intact core incubations	(Gihring et al., 2010a)
Gullmarsfjorden, Sweden and Thames Estuary, England	12 - 63	2	Intact core incubations	(Trimmer et al., 2006)
Hypoxic zone off the Changjiang River estuary, China	5 - 15	9	Intact core incubations	(Yang et al., 2022)
Jinpu Bay, China	4.1 - 11.8	12	Continuous-flow experiments	(Yin et al., 2015)
Jiulong River Estuary, China	10 - 695	2	Intact core incubations	(Wan et al., 2023)
Kattegat and Skagerrak	345	10	Intact core incubations	(Rysgaard et al., 2001)
Lawrence estuary	1.5	1	Intact core incubations	(Crowe et al., 2012)
Little Lagoon, USA	NM	1	Continuous-flow experiments	(Bernard et al., 2015)
Noosa River estuary,	0 - 116	5	Intact core	(Chen et al.,

Australia			incubations	2021)
North Sea	31	9	Intact core incubations	(Rosales Villa et al., 2019)
North Sea	9 - 49	1	Intact core incubations	(Fan et al., 2015)
North Sea	29 - 81	8	Intact core incubations	(Bale et al., 2014)
North Sea	41 - 66	16	Intact core incubations	(Neubacher et al., 2011)
Northeast Chukchi Sea	30 - 128	5	Continuous-flow experiments	(McTigue et al., 2016)
Northeastern New Zealand continental shelf	31 - 41	7	Intact core incubations	(Cheung et al., 2024)
Northern Baltic Proper	27.7 - 64.8	17	Intact core incubations	(Bonaglia et al., 2014a)
Northern East China Sea, China	176 - 688	16	Continuous-flow experiments	(Chang et al., 2021)
Norwegian Trench, Skagerrak	NM	4	Intact core incubations	(Trimmer et al., 2013)
Öre Estuary, Swedish	7-26	6	Intact core incubations	(Hellemann et al., 2017)
Pearl River Estuary, China	NM	5	Intact core incubations	(Tan et al., 2019)
Plum Island Sound, Massachusetts	0.5 - 1	4	Intact core incubations	(Koop-Jakobsen and Giblin, 2010)
Randers Fjord and Norsminde Fjord, Denmark	1 - 695	2	Intact core incubations	(Risgaard-Petersen et al., 2004)
Randers Fjord, Young Sound and Skagerrak, Danmark	NM	3	Intact core incubations	(Risgaard-Petersen et al., 2003)
Sacca di Goro lagoon, Italy	1450	6	Intact core incubations	(Magri et al., 2020)
Southern and central Baltic Sea	0.2 - 80	12	Intact core incubations	(Deutsch et al., 2010)
Southern Finland	NM	5	Intact core incubations	(Uusheimo et al., 2018)
St. George Island, Gulf of Mexico, Hausstrand, German Wadden Sea and Spitsbergen island, Svalbard	NM	5	Intact core incubations	(Canion et al., 2014)

St. Joseph Bay, USA	0.82	4	Continuous-flow experiments	(Hoffman et al., 2019)
St. Lawrence Estuary, Canada	NM	3	Intact core incubations	(Poulin et al., 2007)
Stockholm Archipelago, Baltic Sea	28	1	Intact core incubations	(Bonaglia et al., 2014b)
Svalbard, Norway	170 - 869	10	Intact core incubations	(Blackburn et al., 1996)
Taganga Bay, Colombia Caribbean	NM	8	Intact core incubations	(Arroyave Gómez et al., 2020)
Tama Estuary, Japan	20 - 30	2	Continuous-flow experiments	(Usui et al., 2001)
Texas estuaries, USA	0.6 - 3	26	Continuous-flow experiments	(Gardner et al., 2006)
The Baltic Sea	105	1	Intact core incubations	(Bonaglia et al., 2013)
The Curonian Lagoon	1 - 2.5	8	Intact core incubations	(Bartoli et al., 2021)
Tropical Coastal Lagoons	0.2 - 3	11	Intact core incubations	(Enrich-Prast et al., 2016a)
Tropical Coastal Wetlands, Australia	NM	8	Intact core incubations	(Adame et al., 2019b)
Ulleung Basin, East Sea	72 - 2342	9	Intact core incubations	(Na et al., 2018)
Wallis Lake estuary, Australia	NM	2	Intact core incubations	(Erler et al., 2017)
Young Sound fjord, northeast Greenland	40	1	Intact core incubations	(Rysgaard et al., 1996a)

969 NM denotes that water depth is not mentioned.

删除[小子]: Continuous-flow experiments denote continuous flow experiments combined with core incubations