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Recent Advances in Marine Nitrogen Cycling: From Diazotrophy to Denitrification

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ABSTRACT: Marine nitrogen cycling plays a critical role in regulating ocean productivity, biogeochemical fluxes, and the global carbon cycle. This mini-review synthesizes recent advances in understanding nitrogen transformations, from fixation by diverse diazotrophs to losses via denitrification, anammox, and DNRA, highlighting their ecological and biogeochemical significance. Recent studies have revealed the complex interactions between microbial communities and environmental drivers, including nutrient availability, oxygen minimum zones, stratification, and climate-induced warming. Technological innovations such as metagenomics, metatranscriptomics, proteomics, autonomous sensors, and compound-specific isotope analysis have provided unprecedented insights into nitrogen cycling dynamics, allowing high-resolution spatial and temporal assessments. The review also emphasizes the impacts of anthropogenic stressors, including eutrophication, pollution, and emerging contaminants like microplastics, on nitrogen fluxes and microbial function. Despite these advances, substantial uncertainties remain regarding global nitrogen budgets, the ecology of understudied diazotrophs, and the long-term responses of nitrogen cycling processes to climate and human pressures. Future research priorities include expanding long-term autonomous observations, integrating microbial process rates into biogeochemical and Earth system models, and investigating interactions with emerging pollutants. Improved understanding of these processes is essential for accurately predicting ocean productivity, carbon sequestration, and feedbacks to climate change. Collectively, this review underscores the need for interdisciplinary approaches that combine molecular biology, biogeochemistry, and advanced observational technologies to resolve key knowledge gaps and enhance our capacity to manage and predict the functioning of marine nitrogen cycles in a rapidly changing ocean environment.

KEYWORDS: Marine nitrogen cycling; diazotrophy; denitrification; climate change; emerging pollutants

1. Introduction

Nitrogen (N) plays a foundational role in sustaining marine life, serving as an essential element for the synthesis of amino acids, proteins, nucleic acids, and other cellular components. Despite its abundance in the atmosphere as dinitrogen gas (N_2), most marine organisms cannot directly utilize this chemically inert form, making bioavailable nitrogen one of the primary limiting nutrients for ocean productivity [1]. In many regions particularly oligotrophic subtropical gyres, the scarcity of fixed nitrogen constrains phytoplankton growth, shapes microbial community composition, and governs the structure of marine food webs. Consequently, understanding the pathways that regulate nitrogen availability is central to interpreting patterns of ocean productivity, carbon cycling, and ecosystem resilience.

The marine nitrogen cycle comprises a complex network of biological and chemical transformations that mediate the conversion of nitrogen among multiple redox states. These transformations include nitrogen fixation, ammonification, nitrification, denitrification, anaerobic ammonium oxidation (anammox), and dissimilatory nitrate reduction to ammonium (DNRA) [2]. Each pathway is performed by specialized microbial groups that occupy distinct ecological niches, ranging from sunlit surface waters to oxygen-depleted mid-water regions and anoxic sediments. The interplay among these processes determines whether nitrogen is retained within the marine environment or removed through gaseous losses (N_2 or N_2O), ultimately influencing the productivity and biogeochemical functioning of the global ocean.

Traditional understanding of the nitrogen cycle emphasized a few dominant players, such as Trichodesmium for nitrogen fixation and heterotrophic bacteria for denitrification. However, recent advances have disrupted this simplistic view. Cutting-edge molecular techniques, metagenomics, advanced isotope tracers, and autonomous ocean observatories have revealed a dynamic and far more diverse marine nitrogen cycle [3]. For example, new discoveries include abundant non-cyanobacterial diazotrophs, widespread nitrification by ammonia-oxidizing archaea (AOA), and surprising contributions from viruses in regulating nitrogen-transforming microbial communities [4].

Recent research has underscored how sensitive nitrogen cycling is to environmental changes. Climate-driven factors such as ocean warming, stratification, acidification, and deoxygenation significantly alter microbial community structure and process rates [5]. Warming enhances stratification, reducing nutrient upwelling and potentially limiting nitrogen supply to the surface, while expanding OMZs intensify nitrogen loss via denitrification and anammox, disrupting the balance between nitrogen inputs and losses [3, 5]. Human activities also contribute: increased riverine nitrogen loading and coastal eutrophication influence nitrogen availability and stimulate processes like denitrification, potentially leading to hypoxia and altered nitrogen fluxes [6].

Modeling and observational studies are gradually integrating these complex responses into global biogeochemical frameworks. Previous study used a variable-stoichiometry Earth system model including benthic denitrification to show that sediment nitrogen loss strongly influences global N_2 fixation and primary production, highlighting a previously underappreciated feedback between benthic and pelagic nitrogen cycles [3]. Similarly, a comprehensive global database of nitrogen loss rates (denitrification and anammox) in coastal and marine sediments provides critical empirical constraints for improving model parameterizations [7].

Beyond classical microbial pathways, emerging work has begun to explore less conventional drivers of nitrogen cycling. Viruses, for instance, can influence nitrogen transformations by modulating host microbial mortality, horizontal gene transfer, and the expression of nitrogen-cycle–related auxiliary metabolic genes [4]. These viral-mediated interactions represent an exciting frontier in understanding how nitrogen is cycled, regulated, and linked with larger ecosystem functioning.

Given the rapid pace of discovery, synthesizing current knowledge on the marine nitrogen cycle is timely and necessary. This mini-review integrates recent advances from observational, experimental, and modeling approaches to highlight the evolving understanding of nitrogen transformations in the ocean. Specifically, we focus on diazotrophy, nitrification, denitrification, and anammox, and how climate and anthropogenic stressors are reshaping their dynamics. The aim of this mini-review is to provide an updated synthesis of major microbial nitrogen transformation pathways in the marine environment, discuss the implications of recent findings for global biogeochemical cycles, and identify critical knowledge gaps that warrant future research.

2. Review Methodology

2.1. Literature databases.

The literature for this review was systematically gathered from multiple electronic databases, including Web of Science, Scopus, Google Scholar, and PubMed. These databases were selected to ensure comprehensive coverage of peer-reviewed studies across disciplines relevant to marine nitrogen cycling, including marine microbiology, biogeochemistry, and oceanography. In addition to database searches, the reference lists of key articles were screened to identify additional relevant studies that may have been missed during the initial search.

2.2. Search keywords and temporal coverage,

To capture recent advances, the search was restricted to studies published between 2015 and 2025. Keywords were carefully selected to encompass the major nitrogen cycling processes and their ecological, biogeochemical, and technological aspects. These included “marine nitrogen cycle,” “nitrogen fixation,” “diazotrophy,” “denitrification,” “anammox,” “DNRA,” “nitrification,” “ammonia-oxidizing archaea,” “climate change,” and “anthropogenic impacts,” among others. Boolean operators and truncation symbols were applied where appropriate to optimize the search and ensure comprehensive coverage of relevant literature.

2.3. Inclusion and exclusion criteria.

Studies were included if they focused on marine ecosystems, provided empirical, experimental, modeling, or review data on nitrogen transformations, and addressed microbial ecology, environmental drivers, or anthropogenic influences. Exclusion criteria comprised studies restricted to freshwater or terrestrial systems, non-peer-reviewed articles, and publications lacking sufficient methodological or contextual information. This approach ensured that only studies directly relevant to marine nitrogen cycling and its recent advances were considered.

2.4. Data extraction and synthesis.

Relevant data from the selected articles were systematically extracted, emphasizing nitrogen sources, microbial diversity, functional roles, environmental and anthropogenic controls, and technological innovations such as omics approaches, autonomous sensors, and isotope-based techniques. The findings were then organized thematically into subsections corresponding to major nitrogen transformations, environmental and anthropogenic drivers, and emerging research trends. This synthesis approach facilitated a coherent and structured presentation of the current knowledge, highlighted gaps, and identified priorities for future research. Tables were also used to summarize key aspects of nitrogen cycling processes, microbial diversity, and emerging insights to enhance clarity and comparability.

3. Marine Nitrogen Sources and Transformations

Nitrogen (N) entering the ocean originates from a mixture of natural and anthropogenic sources, fueling microbial processes that transform nitrogen among various chemical forms. Understanding these sources and transformations is essential to characterizing the marine nitrogen cycle (Table 1).

Table 1. Major natural nitrogen sources and transformations in marine ecosystems.

Category	Process/Source	Description	Reference
Natural Nitrogen Sources	Atmospheric deposition	Reactive nitrogen (nitrate, ammonium, DON) delivered to surface ocean. Contributes 3–4 % of net primary production in oligotrophic regions; enhanced by shipping and combustion in coastal areas.	[8, 9]
	Upwelling and mixing	Deep waters rich in nitrate and ammonium are transported to surface, sustaining phytoplankton blooms and primary productivity. Vertical transport dominates nutrient availability in productive upwelling zones.	[10]
	Riverine inputs	Rivers transport inorganic (nitrate, ammonium) and organic nitrogen (dissolved and particulate) to coasts. Rivers also mediate in-transit transformations like denitrification and remineralization, influencing coastal productivity and eutrophication.	[11]
Nitrogen Transformations	Nitrogen fixation (diazotrophy)	Diazotrophs convert N_2 gas into bioavailable ammonium. Both cyanobacterial (e.g., *Trichodesmium*) and non-cyanobacterial diazotrophs (NCDs) contribute, including in particle-associated and mesopelagic niches. Symbioses with microalgae enhance fixation in low-nutrient environments.	[12, 13]
	Ammonification	Heterotrophic microbes remineralize organic nitrogen from sinking particles or dissolved organic matter to ammonium, replenishing reduced nitrogen for assimilation or nitrification.	[14]
	Nitrification	Two-step aerobic oxidation: ammonia → nitrite → nitrate. Ammonia-oxidizing archaea (AOA) dominate step 1, even under low-oxygen conditions; some AOA can convert N_2O to N_2, a novel nitrogen-loss pathway.	[15, 16]
	Denitrification	Anaerobic reduction of nitrate to N_2 (via nitrite, nitric oxide, N_2O). Major N-loss mechanism in oxygen-limited environments. Controlled by organic carbon, nitrate availability, and oxygen levels.	[17]
	Anammox	Oxidation of ammonium using nitrite to produce N_2 without organic carbon. Substantial contribution to nitrogen loss in oxygen-minimum zones and sediments; interacts with denitrification to regulate regional N budgets.	[17]
	DNRA (Dissimilatory Nitrate Reduction to Ammonium)	Reduces nitrate to ammonium instead of N_2, retaining nitrogen in the system. Competes with denitrification in sediments with high carbon and low oxygen. Observed at comparable rates to denitrification in polluted regions.	[18]

3.1.Natural nitrogen sources.

Reactive nitrogen (nitrate, ammonium, dissolved organic nitrogen) is delivered to the surface ocean via atmospheric deposition. Although traditionally considered modest compared to riverine inputs, recent studies highlight its growing importance, especially in coastal and marginal sea regions. Measurements in the northwestern Pacific indicate that atmospheric nitrogen deposition can support 3–4 % of net primary production in oligotrophic regions [8]. Emissions from shipping and combustion can also contribute significantly, accounting for up to a third of nitrogen deposition in some coastal regions [9].

Deep ocean waters, rich in nitrate and ammonium, are brought to the surface through upwelling and mixing, particularly in equatorial and coastal systems. This resupply of "old" nitrogen sustains phytoplankton blooms in nutrient-limited waters and supports primary productivity. Regional studies confirm that vertical transport is a dominant mechanism controlling nutrient availability in certain productive upwelling zones [10].

Rivers transport large amounts of inorganic (nitrate, ammonium) and organic nitrogen (dissolved and particulate) to the coastal ocean. Global modeling indicates that rivers deliver substantial nitrogen loads while simultaneously mediating in-transit transformations such as denitrification and organic matter remineralization [11]. Riverine nitrogen remains a major source for coastal productivity and influences eutrophication dynamics in many regions.

3.2.Overview of major nitrogen transformations.

Once in the ocean, nitrogen undergoes microbial transformations that interconvert it among chemical forms, regulating its availability and removal. Diazotrophs convert N_2 gas into bioavailable ammonium. Historically, cyanobacteria like *Trichodesmium* were considered dominant, but non-cyanobacterial diazotrophs (NCDs) are increasingly recognized as significant contributors, particularly in particle-associated niches and mesopelagic waters [12]. Symbiotic interactions between NCDs and microalgae further enhance nitrogen fixation in low-nutrient environments [13].

Organic nitrogen from sinking particles or dissolved organic matter is remineralized to ammonium by heterotrophic microbes. This process replenishes reduced nitrogen in the water column and sediments, providing substrate for nitrification or assimilation, and plays a key role in nutrient recycling [14]. Nitrification is a two-step aerobic process: ammonia is oxidized to nitrite, followed by oxidation of nitrite to nitrate. Ammonia-oxidizing archaea (AOA) dominate the first step and are abundant in bloom conditions, including low-oxygen waters [15]. Recent studies reveal that some AOA can adapt to oxygen depletion, even converting nitrous oxide (N_2O) to N_2, highlighting a novel nitrogen-loss pathway [16].

This anaerobic process sequentially reduces nitrate to nitrite, nitric oxide, nitrous oxide, and finally dinitrogen gas (N_2). Denitrification is a major nitrogen-loss mechanism in oxygen-limited environments. Global databases of sedimentary denitrification rates demonstrate how organic carbon availability, nitrate, and oxygen control spatial patterns of nitrogen removal [17]. Anammox bacteria oxidize ammonium using nitrite to produce N_2, bypassing organic carbon requirements. Anammox contributes substantially to total nitrogen loss, particularly in oxygen-minimum zones and sediments [17]. Spatial partitioning with denitrification determines regional nitrogen budgets.

DNRA reduces nitrate to ammonium rather than N_2, retaining nitrogen in the system. It competes with denitrification in sediments under high carbon availability and low oxygen. Studies in polluted Baltic Sea sediments indicate that DNRA persists at rates comparable to denitrification, highlighting microbial resilience under anthropogenic stress [18]. Collectively, these processes form a complex network of nitrogen retention, recycling, and loss that dynamically responds to environmental drivers. Interactions among pathways, such as DNRA versus denitrification or nitrification coupled to anammox, largely determine the fate of reactive nitrogen in marine ecosystems.

4. Diazotrophy (Nitrogen Fixation)

Nitrogen fixation, or diazotrophy, is the biochemical conversion of atmospheric nitrogen (N_2) into biologically available ammonium (NH_3), supplying "new" nitrogen to the marine ecosystem. Recent advances in molecular tools, high-throughput sequencing, and ecological modeling have transformed our understanding of diazotroph diversity, distribution, and ecological significance (Table 2).

Table 2. Marine diazotrophy: diversity, distribution, and ecological significance.

Category	Aspect	Description	Reference
Diazotroph Diversity	Cyanobacterial Diazotrophs	Historically considered dominant; include *Trichodesmium* and *Crocosphaera*, supplying new nitrogen to oligotrophic waters.	[19,20]
	Non-Cyanobacterial Diazotrophs (NCDs)	Globally widespread; includes Proteobacteria, Planctomycetes, Verrucomicrobia; often particle-associated, can fix N_2 even under oxygenated conditions.	[19,20]
Biogeography & Environmental Controls	Spatial Distribution	Shaped by temperature, nutrients, light, and water mass origin; Kuroshio intrusion affects community composition in northern South China Sea.	[20,21,22]
	Temporal & Seasonal Variation	Influenced by ocean circulation, vertical mixing, and stratification, leading to variability in N_2 fixation rates across regions.	[21,22]
Physiological Plasticity & Ecological Interactions	Metabolic Flexibility	Diazotrophs adjust metabolic traits in response to temperature, nutrients, and light, enabling survival across oligotrophic gyres to nutrient-rich coasts.	[23]
	Symbiotic & Microbial Interactions	Nitrogen fixed by diazotrophs is transferred to associated phytoplankton; transfer efficiency depends on light intensity, supporting microbial food webs and primary productivity.	[24]
Particle-Associated Nitrogen Fixation	Marine Aggregates & Marine Snow	Heterotrophic bacteria attached to particles fix N_2 under variable temperature and oxygen; may contribute up to 10 % of global marine N_2 fixation.	[1]
	Micro-Niches & Nitrogen Transfer	Particles provide microenvironments favorable for nitrogenase activity and facilitate nitrogen sharing within the microbial community.	[1]

4.1. Diversity of marine diazotrophs.

Historically, cyanobacteria such as *Trichodesmium* were considered the primary contributors to marine N_2 fixation. However, recent metagenomic analyses reveal that non-cyanobacterial diazotrophs (NCDs) are globally widespread and may contribute significantly to nitrogen budgets. Delmont et al. [19] identified 40 heterotrophic bacterial diazotrophs in the sunlit ocean, including members of Proteobacteria, Planctomycetes, and Verrucomicrobia. These organisms are often particle-associated, forming microenvironments that facilitate nitrogen fixation even under oxygenated conditions. Similarly, Zehr [20] emphasizes the ecological importance of NCDs, especially in low-nutrient and mesopelagic waters, challenging the conventional view that cyanobacteria dominate marine diazotrophy.

4.2. Biogeography and environmental controls.

Global nifH gene surveys and metagenomic datasets show that diazotroph distributions are shaped by multiple environmental factors. Temperature, nutrient availability, light intensity, and water mass origin influence both community structure and activity [20,21]. For example, in the northern South China Sea, Kuroshio intrusion modulates diazotroph community composition, enhancing the abundance of specific nifH phylotypes [22]. Such patterns highlight the role of ocean circulation, vertical mixing, and stratification in determining the spatial and temporal distribution of N_2 fixation.

4.3.Physiological plasticity and ecological interactions.

Diazotrophs exhibit substantial physiological plasticity, adjusting their metabolic traits in response to temperature, nutrient concentration, and light regimes [23]. This plasticity allows both cyanobacterial and heterotrophic diazotrophs to survive across diverse marine habitats, from oligotrophic gyres to nutrient-enriched coastal waters. Co-culture experiments reveal that nitrogen fixed by diazotrophs is transferred to associated phytoplankton, with the transfer efficiency strongly dependent on light intensity [24]. Such interactions underscore the critical role of diazotrophs in supporting microbial food webs and sustaining primary productivity.

4.4.Particle-associated nitrogen fixation.

Recent studies highlight the ecological importance of particle-associated nitrogen fixation. Heterotrophic bacteria attached to marine aggregates, or marine snow, can fix nitrogen under a wide range of temperatures and oxygen levels, including suboxic mesopelagic waters [1]. Modeling suggests that this pathway may contribute up to 10 % of global marine N_2 fixation, revealing a previously underestimated component of the nitrogen cycle. Particle association not only provides micro-niches favorable for nitrogenase activity but also facilitates nitrogen transfer to other microorganisms within the aggregate.

5. Ammonification and Nitrification

Ammonification and nitrification are key processes in the marine nitrogen cycle, mediating the transformation of organic nitrogen to inorganic forms that are bioavailable or subject to further oxidation. Both processes are tightly coupled, influencing nutrient availability, nitrogen retention, and ecosystem productivity (Table 3).

5.1.Ammonification (mineralization).

Ammonification, or mineralization, refers to the microbial decomposition of organic nitrogen compounds into ammonium (NH_4^+), which can then be assimilated by primary producers or oxidized via nitrification. This process occurs throughout the water column, sediments, and in association with detrital particles. Recent studies emphasize the role of microbial community composition in controlling ammonification rates. For example, metagenomic analyses in subtropical and coastal oceans demonstrate that heterotrophic bacteria from the phyla Proteobacteria and Bacteroidetes dominate organic nitrogen mineralization, particularly in particle-associated microenvironments [25].

Environmental factors strongly regulate ammonification. Temperature, oxygen concentration, and organic matter quality influence both microbial abundance and enzyme activity. In mesopelagic zones of the North Atlantic, ammonification rates were observed to increase with higher temperatures, highlighting potential feedbacks under climate warming [26]. Similarly, oxygen-depleted zones exhibit altered ammonification dynamics, as facultative anaerobes contribute more to nitrogen recycling under hypoxic conditions.

Ammonification is also tightly linked to carbon-nitrogen interactions. Labile organic carbon availability enhances microbial decomposition of organic nitrogen, whereas recalcitrant compounds slow the process [27]. This coupling underscores the importance of considering both carbon and nitrogen dynamics when modeling nutrient fluxes in marine ecosystems.

Table 3. Ammonification and nitrification in marine nitrogen cycling.

Category	Process	Description	Reference
Ammonification (Mineralization)	Microbial decomposition	Organic nitrogen is converted into ammonium (NH_4^+) by heterotrophic bacteria (Proteobacteria, Bacteroidetes) throughout the water column, sediments, and particle-associated microenvironments.	[25]
	Environmental controls	Temperature, oxygen, and organic matter quality regulate ammonification rates. Higher temperatures and labile carbon enhance mineralization; hypoxia shifts dynamics toward facultative anaerobes.	[26, 27]
	Carbon–Nitrogen coupling	Ammonification is linked to labile organic carbon availability; recalcitrant carbon slows N mineralization. This interaction affects nutrient flux modeling and nitrogen retention.	[27]
Nitrification	Step 1: Ammonia → Nitrite	Oxidation of NH_4^+ to NO_2^- primarily by ammonia-oxidizing archaea (AOA) and bacteria (AOB); AOA dominate most marine environments, especially oligotrophic waters.	[28]
	Step 2: Nitrite → Nitrate	Nitrite-oxidizing bacteria (NOB) oxidize NO_2^- to NO_3^-. Links ammonification to nitrogen-loss processes such as denitrification and anammox.	[28, 29]
	Environmental controls	Nitrification is influenced by oxygen, light, and nutrient levels; can occur under low oxygen in OMZs via high-affinity pathways.	[29]
	Greenhouse gas production	Nitrifying microbes can produce nitrous oxide (N_2O) as a byproduct, contributing to marine greenhouse gas emissions in coastal and open-ocean systems.	[30]
	Particle-associated nitrification	Marine aggregates create micro-niches supporting localized nitrification in low-oxygen zones, highlighting the importance of micro-scale processes.	[25]
	Modeling insights	Variations in ammonium supply from ammonification regulate nitrification rates, modulating nitrate availability and downstream nitrogen loss via denitrification and anammox.	[26, 27]

5.2.Nitrification.

Nitrification is a two-step aerobic process that oxidizes ammonium first to nitrite (NO_2^-) and then to nitrate (NO_3^-). It is primarily mediated by two groups of microorganisms: ammonia-oxidizing archaea (AOA) and bacteria (AOB) for the first step, and nitrite-oxidizing bacteria (NOB) for the second. Recent molecular surveys indicate that AOA dominate ammonia oxidation in most marine environments, often outnumbering AOB by orders of magnitude, particularly in oligotrophic waters [28].

Nitrification plays a crucial role in connecting ammonification to nitrogen loss processes such as denitrification and anammox. Recent studies show that nitrification rates are influenced by oxygen availability, light, and nutrient concentrations. For instance, nitrification can occur at low oxygen concentrations in oxygen minimum zones, where some AOA exhibit high-affinity oxygen-utilizing pathways [29]. Moreover, nitrifying microbes can produce nitrous oxide (N_2O) as a byproduct, linking nitrification to greenhouse gas emissions in coastal and open-ocean systems [30].

Particle-associated nitrification is another emerging area of research. Marine aggregates provide micro-niches with gradients of oxygen and ammonium, supporting localized nitrification even in low-oxygen environments [25]. Such micro-scale processes can have disproportionately large impacts on nitrogen cycling, emphasizing the importance of studying both bulk water and particulate microenvironments.

Recent modeling efforts incorporate ammonification and nitrification dynamics into global biogeochemical frameworks. These models demonstrate that variations in ammonium supply from mineralization directly regulate nitrification rates, which in turn modulate nitrate availability and subsequent nitrogen loss through denitrification or anammox [26,27]. Understanding these couplings is critical for predicting how nitrogen fluxes may respond to climate change and anthropogenic inputs.

6. Denitrification and Anammox

Nitrogen loss pathways in the marine environment are critical in regulating the overall nitrogen budget, ecosystem productivity, and greenhouse gas emissions. Denitrification, anammox, and dissimilatory nitrate reduction to ammonium (DNRA) are the main microbial processes driving nitrogen removal or recycling under varying redox conditions.

6.1.Denitrification.

Denitrification is the sequential reduction of nitrate (NO_3^-) to nitrite (NO_2^-), nitric oxide (NO), nitrous oxide (N_2O), and finally dinitrogen gas (N_2). This anaerobic process occurs predominantly in oxygen-depleted waters and sediments, and is mediated by a diverse assemblage of heterotrophic bacteria. Recent studies have quantified denitrification rates across coastal and open-ocean sediments, demonstrating that rates are strongly influenced by nitrate availability, organic carbon supply, and oxygen concentration [31]. In the Eastern Tropical South Pacific, oxygen minimum zones (OMZs) sustain high denitrification rates, contributing significantly to global nitrogen loss [32]. Furthermore, denitrification is a major source of N_2O, a potent greenhouse gas. Experimental studies in hypoxic coastal sediments indicate that N_2O yield varies with nitrate concentrations and microbial community composition [33]. Denitrification is also affected by anthropogenic nutrient inputs. Coastal eutrophication can stimulate denitrification initially, but prolonged organic matter enrichment may shift microbial communities toward DNRA, reducing net nitrogen removal [34]. These dynamics underscore the interplay between environmental conditions, microbial ecology, and nitrogen fluxes.

6.2.Anammox (anaerobic ammonium oxidation).

Anammox is an anaerobic process in which ammonium (NH_4^+) is oxidized using nitrite (NO_2^-) as the electron acceptor to produce N_2 gas. Anammox bacteria, belonging to the phylum Planctomycetota, are prevalent in oxygen-depleted waters, sediments, and marine aggregates. Recent advances in molecular detection (e.g., 16S rRNA and hzsA gene surveys) have highlighted the widespread contribution of anammox to marine nitrogen loss. In the Arabian Sea OMZ, anammox can account for up to 50% of total N_2 production, demonstrating its global significance [35]. Environmental drivers, such as nitrite availability, oxygen levels, and organic carbon concentration, regulate anammox activity. Importantly, anammox is often tightly coupled to nitrification, as ammonium produced by ammonification or regeneration fuels both nitrification and subsequent anammox [36]. Anammox is also sensitive to anthropogenic impacts. Coastal pollution and eutrophication can modify sediment redox profiles, potentially altering anammox rates and nitrogen retention. Studies suggest that understanding anammox distribution is essential for accurate modeling of nitrogen budgets under changing environmental conditions.

6.3.Dissimilatory nitrate reduction to ammonium (DNRA).

DNRA is an anaerobic microbial process that reduces nitrate to ammonium rather than gaseous N_2, retaining bioavailable nitrogen within the system. DNRA competes with denitrification for nitrate, and the relative dominance of each pathway depends on carbon-to-nitrate ratios, oxygen levels, and microbial community composition [37]. Recent field studies in coastal and estuarine sediments indicate that DNRA can account for 20–60% of nitrate reduction in high-carbon environments, especially in eutrophic systems [38]. DNRA is therefore a nitrogen-retention process, counteracting the nitrogen loss driven by denitrification and anammox. Its activity also influences nutrient recycling, primary production, and ecosystem resilience. Emerging evidence suggests that microbial communities capable of DNRA are highly adaptable, enabling nitrogen recycling under environmental stress such as hypoxia and pollution [39]. Understanding the balance among denitrification, anammox, and DNRA is critical for predicting marine nitrogen cycling under future climate change and anthropogenic perturbations. Integration of molecular, biogeochemical, and modeling approaches is advancing knowledge of nitrogen removal pathways and their ecological consequences.

7. Emerging Themes and Recent Advances

7.1.Climate change impacts.

Ocean warming effects on N fixation. Rising sea surface temperatures strongly influence diazotroph physiology and distribution. Modeling studies integrating empirical energetics show that warming increases the elemental-use efficiency (EUE) of key diazotrophs, such as *Trichodesmium* and *Crocosphaera*, allowing nitrogen fixation with lower iron and phosphorus demand, potentially expanding diazotroph niches poleward. Earth system modeling also indicates that enhanced benthic denitrification under warming may feedback on surface nitrogen inventories and global primary production [40]. Stratification and nutrient redistribution. Climate-driven stratification in the upper ocean limits nutrient upwelling, reducing supply of essential elements like phosphate and iron for diazotrophs. Reduced vertical mixing can enhance retention of regenerated nitrogen in the euphotic zone, modifying the balance between new nitrogen inputs and internal recycling [41]. This can shift community composition toward organisms adapted to low-nutrient, stable conditions. OMZ expansion and enhanced N loss. Oxygen minimum zones (OMZs) are projected to expand with warming, intensifying anaerobic nitrogen loss via denitrification and anammox. Recent studies show that nitrate reduction and nitrite oxidation may dominate over classical denitrification in some OMZs, highlighting shifts in nitrogen loss pathways and altering the efficiency of the biological pump [42, 43]. Observations in polar regions also indicate that N_2 fixation persists under seasonal ice, with non-cyanobacterial diazotrophs contributing to high-latitude nitrogen inputs

[41]. Table 4 shows the emerging themes, recent advances, and knowledge gaps in marine nitrogen cycling.

Table 4. Emerging themes, recent advances, and knowledge gaps in marine nitrogen cycling.

Category	Subsection	Key Points	Reference
Climate Change Impacts	Ocean warming	Increases elemental-use efficiency of key diazotrophs (Trichodesmium, Crocosphaera), expands niches poleward, affects benthic denitrification and surface N inventories.	[40]
	Stratification & nutrient redistribution	Limits upwelling, reduces phosphate and iron supply; enhances retention of regenerated nitrogen, favoring low-nutrient-adapted communities.	[41]
	OMZ expansion & enhanced N loss	Expanding OMZs increase anaerobic N loss via denitrification and anammox; shifts in nitrate reduction and nitrite oxidation pathways alter efficiency of the biological pump.	[42, 43]
Anthropogenic Influences	Eutrophication	Nutrient loading accelerates eutrophication; seasonal hypoxia can enhance benthic N fixation, counteracting N loss and exacerbating nutrient accumulation.	[44]
	Pollution effects	Acidification and chemical pollutants modify microbial activity; nitrifiers upregulate pH homeostasis genes, increasing N_2O emissions.	[44]
	Altered Fe & P availability	Human-induced changes in iron and phosphorus inputs affect diazotroph growth; models show iron limitation modulates N_2 fixation under warming.	[45]
Technological Advances	Omics	Metagenomics, metatranscriptomics, proteomics reveal active N-cycling genes, virus-mediated processes, and functional microbial interactions.	[41, 46]
	Autonomous sensors & bio-optics	Floats, gliders, and optical platforms provide high-resolution measurements of nitrate, oxygen, pH, and PON; allow spatial-temporal N flux estimates.	[47, 48]
	Compound-Specific Isotope Analysis (CSIA)	Traces N sources and pathways; $\delta^{15}N$ in amino acids helps differentiate aerobic/anaerobic processes and nitrogen recycling.	[49–51]
Knowledge Gaps & Future Directions	Global N fixation uncertainty	N_2 fixation estimates still vary widely (100–170 Tg N yr^{-1}); uncertainty limits confidence in N budgets relative to denitrification and anammox.	[52, 53]
	Understudied diazotroph communities	Non-cyanobacterial diazotrophs poorly constrained; responses to Fe, P, oxygen remain unquantified.	[54]
	Long-term autonomous observations	Lack of sustained seasonal-to-decadal datasets limits detection of slow or episodic changes in N fixation, nitrification, and loss.	[55]
	Model integration	Current biogeochemical models oversimplify microbial processes; need explicit simulation of diversity, metabolic regulation, and environmental control.	[55]
	Microplastics & emerging pollutants	Microplastics alter sediment microbial communities, affect nitrification/denitrification, and may enhance N_2O emissions; impacts on ocean-wide N cycling remain poorly understood.	[56, 57]

7.2.Anthropogenic influences.

Eutrophication and altered N cycles. Human-induced nutrient loading from agriculture, wastewater, and atmospheric deposition accelerates eutrophication in coastal ecosystems. Seasonal hypoxia can enhance benthic nitrogen fixation, counteracting nitrogen loss via denitrification or anammox, potentially exacerbating nutrient accumulation [44]. Pollution effects on nitrifiers and denitrifiers. Acidification and pollutants modify microbial activity. Metatranscriptomic evidence demonstrates that nitrifiers upregulate pH-homeostasis genes under acidified conditions, leading to higher N_2O production [44]. Such shifts have implications for nitrogen cycling and greenhouse gas emissions. Altered Fe and P availability affecting diazotrophy. Human activities alter iron and phosphorus inputs, which control diazotroph growth. Models including dynamic iron cycles show that ignoring iron limitation overestimates nitrogen fixation under warming, while including it predicts more moderate changes [45]. Changes in nutrient stoichiometry and availability may reshape diazotroph communities and influence non-cyanobacterial nitrogen fixation.

7.3.Technological advances.

Omics (metagenomics, metatranscriptomics, proteomics). ‘Omics approaches have revolutionized nitrogen cycling research. A metagenomic study of an Arctic bloom revealed active transcription of nitrogen-cycling genes during seasonal phytoplankton growth [41]. Viral metagenomics also indicates that viruses contribute to nitrogen cycling via host lysis and auxiliary metabolic genes influencing nitrification, denitrification, and anammox [46]. Autonomous sensors and bio-optical platforms. High-resolution data from floats, gliders, and autonomous sensors provide continuous measurement of nitrate, oxygen, pH, and bio-optical properties [47]. Algorithms linking particulate organic nitrogen (PON) to optical properties allow estimation of nitrogen export and cycling over broad spatial and temporal scales [48]. Compound-specific isotope analysis (CSIA). CSIA offers precision in tracing nitrogen sources and pathways. Amino acid $\delta^{15}N$ analyses in fish and microbial samples provide insights into nitrogen recycling, trophic interactions, and anaerobic metabolism [49,50,51]. CSIA allows differentiation between aerobic and anaerobic nitrogen pathways under environmental stress.

8. Knowledge Gaps and Future Directions

Despite rapid progress, significant uncertainties in global nitrogen (N) fixation and loss estimates remain a major barrier to improving biogeochemical models. Recent database compilations indicate that global marine N_2 fixation rates still span a wide range, roughly 100–170 Tg N yr^{-1}, revealing substantial disagreement among measurements and methods [52]. This uncertainty undermines confidence in N-cycle budgets, especially when compared to estimated N losses via denitrification and anammox, which in some models exceed inputs, raising questions about balance and long-term N stability [53].

Closely related is the fact that many diazotroph communities remain understudied, particularly non-canonical and non-cyanobacterial groups. While increased sampling has expanded our understanding, recent reviews emphasize that the ecology, physiology, and genetic regulation of key diazotrophs are still poorly constrained [54]. For example, the response of different diazotroph lineages to environmental gradients such as iron, phosphorus, or oxygen often remains unquantified, limiting our ability to predict how their contributions will shift under future conditions.

Another critical gap is the lack of long-term autonomous observations of nitrogen cycling. Although float and glider platforms now measure parameters such as nitrate and oxygen, sustained datasets that resolve seasonal-to-decadal variability in fixation, nitrification, and loss are still rare. Without these long-term observations, detecting slow or episodic changes such as shifts in N_2 fixation linked to climate drivers, remains challenging.

Closely tied to observation gaps is the need for better integration of microbial process rates into Earth system and biogeochemical models. Current models often use simplified parameterizations or fixed rates for processes like diazotrophy and denitrification, lacking mechanistic links to microbial ecology or environmental control [55]. Advances in modeling that explicitly simulate microbial diversity, metabolic regulation, and competition could significantly improve predictions of nitrogen flux responses under global change.

An emerging frontier is the interaction between the N cycle and microplastics or other emerging pollutants. Recent microcosm experiments show that microplastic particles can significantly alter sediment microbial community composition and enhance or suppress nitrification and denitrification, depending on polymer type [56]. In estuarine systems, microplastics have been linked to elevated production of nitrous oxide (N_2O) by nitrifiers and incomplete denitrification, suggesting these pollutants may amplify greenhouse gas emissions [57]. Yet, little is known about how widespread these effects are across oceanic systems, how microplastics influence functional gene abundance, or how they interact with other stressors.

Addressing these gaps will require coordinated efforts. First, increasing in situ measurements of nitrogen fixation using geochemical tracers (such as $\delta^{15}N$) and molecular tools in under-sampled regions especially OMZs and polar oceans, is essential. Second, expanding autonomous biogeochemical platforms and integrating them with targeted incubation experiments can help build long-term datasets. Third, models need to evolve to incorporate microbial traits, regulatory networks, and pollutant stressors. Finally, interdisciplinary research combining microbiology, biogeochemistry, pollution science, and modeling is needed to assess how microplastics and chemical contaminants interact with nitrogen-transforming communities.

9. Implications for Policy and Management

The synthesis of recent advances in marine nitrogen cycling has several direct implications for policymakers, coastal managers, and other stakeholders involved in marine governance. First, understanding the spatial and temporal dynamics of nitrogen fixation, nitrification, denitrification, and anammox processes can inform nutrient management strategies in eutrophication-prone coastal waters, where excessive nitrogen inputs drive hypoxia and harmful algal blooms [58, 59]. Reducing riverine nitrogen loads through integrated watershed and coastal planning can mitigate these impacts and enhance water quality. Second, the incorporation of advanced observational tools such as autonomous sensors, bio-optical platforms, and compound-specific isotope analysis into routine monitoring programs can provide high-resolution, near-real-time assessments of nitrogen fluxes, enabling more proactive decision-making and adaptive management under changing environmental conditions [60, 61]. Third, insights into the sensitivity of nitrogen cycling pathways to climate-driven stressors, such as warming, stratification, and expanding oxygen-minimum zones, underscore the need for adaptive policy frameworks that account for shifting nutrient dynamics under future climate scenarios. Finally, emerging evidence that contaminants like microplastics alter microbial nitrogen transformations highlights the importance of integrating pollutant control and ecological risk assessment into coastal and marine policy agendas [60, 62]. Translating mechanistic understanding of nitrogen cycle processes into actionable strategies can improve ecosystem resilience, support sustainable resource use, and strengthen climate adaptation and mitigation efforts.

Conclusions

Marine nitrogen cycling is a central component of oceanic biogeochemical processes, regulating primary productivity, nutrient availability, and the global carbon cycle. Recent advances have significantly improved our understanding of the pathways and transformations that control nitrogen dynamics, from nitrogen fixation by diazotrophs to nitrogen losses via denitrification, anammox, and DNRA. Research has highlighted the diversity and functional roles of microbial communities in mediating these processes, including both cyanobacterial and non-cyanobacterial diazotrophs, as well as nitrifying and denitrifying bacteria. Technological innovations, such as metagenomics, metatranscriptomics, autonomous biogeochemical sensors, and compound-specific isotope analyses, have enabled high-resolution monitoring and deeper insight into the spatial and temporal variability of nitrogen cycling, revealing previously unrecognized processes and environmental drivers. Climate change and anthropogenic activities are reshaping nitrogen cycling in profound ways. Ocean warming, stratification, and the expansion of oxygen minimum zones are altering nitrogen fixation and loss rates, while human-induced nutrient loading, pollution, and emerging contaminants like microplastics are modifying microbial activity and nitrogen fluxes. These changes have direct consequences for marine productivity, carbon sequestration, and greenhouse gas emissions, emphasizing the interconnectedness of nitrogen cycling with global climate and ecosystem health. Despite substantial progress, critical knowledge gaps remain, including uncertainties in global nitrogen budgets, limited understanding of understudied microbial communities, and a lack of long-term, high-resolution observational datasets. Addressing these gaps through integrated observational, experimental, and modeling approaches is essential for accurate predictions of oceanic nitrogen dynamics under future climate scenarios. Strengthening our capacity to monitor, model, and manage nitrogen cycling will improve our understanding of marine ecosystem resilience and enhance our ability to anticipate and mitigate the impacts of global change on ocean biogeochemistry.

Author Contributions

Chinedu Okafor: Conceptualization, methodology, formal analysis, writing – original draft, supervision; Aisha Bello: Data curation, investigation, visualization, writing – review & editing.

Competing Interests

The authors declare that they have no competing interests.

Data Availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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