

Nitrogen's Role in Toxic Algal Bloom Development in Aquatic Ecosystems

DONALD UGBONG UGBE¹, VICTORIA CHIOMA AYOZIE-SAMUEL², ERNEST, CHIDOZIE IHEANYI³, FRANK CHIBUZOR OKENMUO⁴, LINNET NYOKABI WAHOME⁵, BELLO ALIYU⁶

College of Ecology and Environment, Chengdu University of Technology, China.

Dangote Agricultural Services, Dangote Fertiliser Limited, Lagos, Nigeria.

Department of Soil Science, Chukwuemeka Odumegwu Ojukwu University, Igbariam, Nigeria

College of Computer and Cyber Security, Chengdu University of Technology, China

College of Earth Science, Chengdu University of Technology, Chengdu, China.

Abstract—Harmful algal blooms (HABs) constitute one of the most pressing water quality challenges confronting aquatic ecosystems globally, with nitrogen pollution serving as a fundamental driver of bloom development and persistence. This comprehensive review examines the multifaceted relationships between nitrogen availability and toxic algal bloom formation across freshwater and marine environments. Anthropogenic nitrogen inputs from agricultural runoff, wastewater discharge, and atmospheric deposition have fundamentally altered nutrient dynamics in water bodies worldwide, creating conditions that systematically favor bloom-forming species over diverse phytoplankton communities. The chemical form of nitrogen, whether nitrate, ammonium, or organic compounds differentially influences algal community composition, with various taxa exhibiting distinct preferences and competitive advantages under specific nitrogen regimes. Temporal patterns of nitrogen delivery, from pulsed agricultural runoff to chronic wastewater discharge, shape seasonal bloom dynamics and species succession patterns. Interactions between nitrogen and phosphorus create complex co-limitation scenarios that determine which organisms dominate under given environmental conditions, while nitrogen availability directly influences cellular toxin production in cyanobacteria, dinoflagellates, and diatoms through metabolic regulatory pathways. Climate change intensifies these nitrogen-driven processes through warming, altered precipitation patterns, and strengthened water column stratification. Management strategies encompassing agricultural best practices, wetland restoration, and advanced wastewater treatment show promise for bloom mitigation, though implementation faces substantial economic, political, and technical challenges. The slow recovery of eutrophic systems due to legacy sediment nutrients demands sustained commitment to load reduction over decadal timescales.

Keywords— Algae Bloom, Eutrophication, Cyanobacteria, climate change.

I. INTRODUCTION

1.1 Background and Global Context

Aquatic ecosystems worldwide face mounting pressure from excessive nutrient inputs, particularly nitrogen compounds that fuel massive proliferations of phytoplankton known as harmful algal blooms (HABs). These events devastate marine and freshwater environments, killing fish populations, contaminating drinking water supplies, and producing toxins that sicken humans and wildlife (Huisman et al., 2018). The ecological and economic consequences extend beyond immediate bloom impacts to include long-term habitat degradation, loss of fisheries productivity, and costs associated with water treatment and healthcare (Anderson et al., 2021). The transformation of pristine waters into turbid, toxic environments typically begins with human activities that flood ecosystems with reactive nitrogen. Agricultural runoff carries nitrate from fertilized fields, wastewater treatment plants discharge ammonium-rich effluent, and atmospheric deposition delivers oxidized nitrogen from fossil fuel combustion. These anthropogenic sources have doubled global nitrogen inputs to coastal waters over the past century, creating conditions that favor bloom-forming species over the diverse communities that typically inhabit healthy aquatic systems (Glibert, 2020).

1.2 Nitrogen as a Primary Driver

Understanding nitrogen's multifaceted influence on bloom formation requires examining how different nitrogen species affect algal physiology, competition dynamics, and toxin production across varied environmental contexts. Nitrogen availability shapes which organisms dominate aquatic food webs through several interconnected mechanisms. Many bloom-forming species possess physiological adaptations that allow them to outcompete other phytoplankton when specific nitrogen forms become

abundant. Some dinoflagellates and cyanobacteria can access organic nitrogen compounds that remain unavailable to diatoms and green algae. Others exploit fluctuating nitrogen supplies through luxury uptake and storage mechanisms that provide competitive advantages during subsequent limitation periods (Anderson et al., 2021).

1.3 The Toxicity Dimension

The relationship between nitrogen and algal toxicity adds another critical dimension to this problem. Research demonstrates that nitrogen availability influences not just bloom magnitude but also the toxin content of individual cells (Harke et al., 2016). Cyanobacteria producing microcystins, dinoflagellates synthesizing saxitoxins, and diatoms generating domoic acid all show altered toxicity under different nitrogen regimes, though the specific responses vary by species and environmental conditions (Trainer et al., 2020). This means that, managing bloom risks requires addressing both population size and cellular toxin concentrations objectives that may conflict under certain nutrient reduction scenarios.

1.4 Objectives and Scope

This review synthesizes current understanding of nitrogen's role in harmful algal bloom development, examining nitrogen chemistry and bioavailability, taxon-specific acquisition strategies, temporal supply dynamics, phosphorus interactions, toxin production mechanisms, climate change interactions, and management implications. The analysis draws from field observations, experimental studies, and long-term monitoring programs to provide a comprehensive assessment of nitrogen-bloom relationships relevant to environmental managers, policymakers, and researchers.

II. NITROGEN CHEMISTRY AND BIOAVAILABILITY

2.1 Chemical Forms and Transformations

Aquatic nitrogen exists in multiple chemical forms with distinct biogeochemical behaviors and biological availabilities. The nitrogen cycle in water bodies involves continuous transformations between oxidized forms like nitrate (NO_3^-), reduced forms like ammonium (NH_4^+), and organic nitrogen compounds ranging from simple amino acids to complex dissolved organic matter (Dai et al., 2021). Each form exhibits unique transport characteristics, residence

times, and uptake kinetics that influence competitive outcomes among phytoplankton taxa.

2.2 Nitrate: The Agricultural Legacy

Nitrate represents the most oxidized inorganic nitrogen form in aerobic waters. Rivers draining agricultural watersheds often carry nitrate concentrations exceeding 10 milligrams per liter, far above natural background levels typically below 0.1 mg/L (Van Meter et al., 2021). Fertilizer application rates frequently exceed crop nitrogen requirements, with surplus nitrogen leaching through soil profiles to groundwater or washing from fields during precipitation events. Subsurface tile drainage systems installed across millions of hectares of cropland accelerate this transport, delivering nitrate to streams within hours or days of rainfall. Algae acquire nitrate through active transport systems that require cellular energy expenditure. Once inside cells, nitrate reductase enzymes convert nitrate to nitrite, then nitrite reductase reduces it further to ammonium before incorporation into amino acids (Flynn et al., 2022). This multi-step reduction process consumes reducing equivalents generated through photosynthesis or respiration, creating energetic costs that influence competitive dynamics when alternative nitrogen sources are available.

2.3 Ammonium: Energetically Favorable

Ammonium occurs naturally through decomposition of organic matter and excretion by aquatic animals, but human activities dramatically elevate concentrations through sewage discharge and agricultural waste (Glibert et al., 2022). Being already in reduced form, ammonium can be incorporated directly into organic molecules without the energetic costs of nitrate reduction. Most phytoplankton preferentially consume ammonium when both nitrogen forms are available, suppressing nitrate uptake through a regulatory phenomenon called ammonium inhibition. This preference has significant ecological consequences because ammonium tends to remain near sources of input rather than dispersing like nitrate. In stratified water bodies, ammonium accumulates in bottom waters where organic matter decomposition occurs, creating vertical gradients that influence species distributions. Organisms capable of accessing these deeper ammonium pools while remaining in sufficient light for photosynthesis gain competitive advantages over those restricted to surface waters (Li et al., 2023).

2.4 Organic Nitrogen: An Expanding Frontier

Organic nitrogen comprises dissolved compounds like urea, amino acids, and nucleotides, plus particulate matter including detritus and living organisms. In oligotrophic systems with low inorganic nitrogen, organic compounds can provide the dominant nitrogen source for phytoplankton growth (Bronk et al., 2007). The bioavailability of organic nitrogen varies enormously depending on molecular structure and size. Simple molecules like urea support rapid algal growth, while complex humic substances release nitrogen slowly or remain biologically inert despite representing substantial nitrogen pools.

Many bloom-forming species possess enzyme systems that cleave nitrogen from organic molecules unavailable to competitors. Cyanobacteria produce urease enzymes that hydrolyze urea, while some

dinoflagellates secrete extracellular proteases that break down proteins into absorbable amino acids (Stoecker and Lavrentyev, 2018). The ability to access organic nitrogen expands the nutritional niche of these organisms, allowing growth even when inorganic nitrogen becomes scarce (Cai et al., 2021).

Agricultural and urban runoff increasingly delivers anthropogenic dissolved organic nitrogen (DON) including herbicide metabolites, pharmaceutical residues, and industrial byproducts. The ecological effects of these novel nitrogen compounds remain poorly understood, though evidence suggests some may selectively stimulate particular bloom-forming taxa (Glibert et al., 2026). Wastewater effluent contains substantial DON fractions that conventional treatment processes do not remove, potentially supporting algal growth even in systems receiving advanced treatment for inorganic nitrogen removal.



A shows no green, blue-green or red water surface while B shows blue-green coloration, with a dense bloom of toxic nutrient, with a dead Buffalo (*Bubalus bubalis*).

III. NITROGEN LIMITATION AND ALGAL GROWTH DYNAMICS

3.1 The Limitation Concept

The concept of nutrient limitation proves central to understanding bloom development. In many aquatic systems, nitrogen availability constrains primary production more than light, temperature, or other growth factors (Elser et al., 2007). When nitrogen limitation is relieved through pollution inputs, algal biomass can increase dramatically within days as cells respond to elevated resource availability (Paerl et al., 2016). The specific nitrogen concentration that

triggers this response varies among ecosystems and seasons, but general patterns emerge from comparing oligotrophic and eutrophic conditions.

3.2 Oligotrophic Conditions: Natural Diversity

Oligotrophic lakes and coastal waters typically contain dissolved inorganic nitrogen (DIN) below 10 micrograms per liter. Under these conditions, phytoplankton biomass remains low and species diversity stays high (Smith, 2003). Fast-growing diatoms and chlorophytes dominate, rapidly consuming nitrogen pulses before reverting to nitrogen-starved conditions. This boom-bust pattern prevents any single species from establishing prolonged dominance.

The phytoplankton community turns over quickly, supporting productive food webs without

accumulating high biomass concentrations (Reynolds, 2006). Zooplankton grazers efficiently consume algal production, transferring energy to higher trophic levels while maintaining clear water conditions. Nutrient recycling through grazer excretion provides a continuous but modest nitrogen supply that sustains moderate productivity without triggering blooms. These oligotrophic systems exhibit high ecological resilience, recovering quickly from disturbances and maintaining diverse biological communities.

3.3 Mesotrophic Transitions: Enhanced Productivity

As nitrogen inputs increase, systems transition through mesotrophic conditions where moderate enrichment sustains higher standing stocks of algae. Diatom blooms may occur during spring mixing events that combine nutrient resupply with adequate light availability (Sommer et al., 2012). These blooms typically remain benign because diatoms produce few toxins and provide nutritious food for zooplankton grazers.

The increased productivity supports larger fish populations and enhanced recreational fisheries, creating what many stakeholders initially perceive as desirable ecosystem states (Jeppesen et al., 2005). However, mesotrophic conditions represent transitional states vulnerable to further degradation. Additional nitrogen loading can rapidly push these systems across thresholds, into eutrophic conditions characterized by problematic blooms. Management becomes more challenging as stakeholder groups develop conflicting interests—anglers, benefiting from enhanced fish production may resist nutrient reduction efforts, that water quality managers consider necessary for bloom prevention.

3.4 Eutrophic Systems: Blooms Emerge

Eutrophic conditions emerge when chronic nitrogen loading maintains elevated concentrations through growing seasons. In these enriched systems, nitrogen limitation becomes intermittent rather than continuous (Conley et al., 2009). Cyanobacteria and dinoflagellates increasingly outcompete diatoms because they possess physiological traits suited to fluctuating resource environments (Paerl and Otten, 2013). Their ability to migrate vertically through the water column, fix carbon at depth while accessing nutrients, and store nutrients in cellular reserves provides competitive advantages in stratified,

nitrogen-rich waters. Dense blooms develop that shade underlying waters, reducing light penetration to depths where submersed aquatic vegetation historically thrived. Decomposition of senescent bloom biomass creates oxygen-depleted bottom layers that exclude fish and benthic invertebrates (Smith et al., 2021). Water quality deteriorates substantially, with taste and odor problems affecting drinking water supplies and recreational values declining as users avoid contact with surface scums.

3.5 Hypereutrophic Degradation: Ecological Collapse

Hypereutrophic systems experience severe and persistent nitrogen over-enrichment. Blooms occur regularly and sometimes year-round in warm climates (Chorus and Welker, 2021). Species capable of reaching extreme cell densities dominate, including toxic cyanobacteria like *Microcystis aeruginosa* and *Anabaena circinalis*. These organisms form surface scums containing millions of cells per milliliter, creating dense mats that completely cover water surfaces during peak bloom periods. Water quality deteriorates catastrophically, with pH swings between extreme values disrupting physiological processes in aquatic organisms. Daytime photosynthesis removes dissolved carbon dioxide, driving pH above 10 and causing calcium carbonate precipitation. Nighttime respiration releases carbon dioxide, dropping pH toward 6 and creating acidic conditions. Oxygen depletion becomes widespread and persistent, eliminating habitat for all but the most tolerant species. Toxin accumulation renders water unusable for drinking, recreation, or wildlife habitat (Steffen et al., 2017). Recovery from hypereutrophic conditions requires sustained nutrient load reduction over decades due to internal loading from accumulated sediment organic matter.

3.6 Episodic Events and Climate Extremes

Episodic events like storms and sewage overflows create short-term nitrogen spikes that can trigger opportunistic blooms. A single large rainfall washing nitrogen from agricultural fields or overwhelming sewer systems can elevate nutrient levels for days or weeks (Paerl et al., 2006). Bloom-forming species with fast growth rates can exploit these transient resource pulses if temperature, light, and stratification conditions permit. Combined sewer overflow events during intense rainfall deliver massive nutrient pulses along with organic matter and pathogens. These

events create ideal conditions for rapid algal growth high nutrients, warm temperatures in summer when storms often occur, and sufficient light if turbidity settles quickly. The increasing frequency of intense precipitation events predicted under climate change scenarios may therefore promote more frequent opportunistic blooms (Reichwaldt and Ghadouani, 2012).

3.7 Internal Nitrogen Cycling: The Legacy Effect

Internal nitrogen cycling within water bodies complicates relationships between external loading and algal response. Sediments accumulate organic nitrogen from years or decades of productivity, creating a legacy pool that slowly decomposes to release ammonium back into overlying water (Søndergaard et al., 2003). This internal loading can sustain blooms even after external inputs decrease substantially. Lakes undergoing eutrophication reversal often continue experiencing blooms for years or decades as legacy nutrients recycle through sediments (Jeppesen et al., 2005). The slow response to load reduction frustrates management efforts and challenges political support for sustained intervention. Stakeholders expecting rapid improvement after implementing expensive best management practices become disillusioned when water quality remains poor for extended periods. This demonstrates how historical nitrogen pollution continues affecting modern water quality through biogeochemical memory stored in sediment organic matter (Meals et al., 2010).

IV. NITROGEN-PHOSPHORUS INTERACTIONS IN BLOOM FORMATION

4.1 Co-limitation Framework

While nitrogen availability directly affects algal growth, interactions with phosphorus create complex co-limitation scenarios that determine bloom outcomes. The nitrogen-to-phosphorus ratio (N:P) in water bodies influences species composition more than absolute concentrations of either nutrient alone (Sterner, 2008). Classical nutrient stoichiometry suggests that phytoplankton require nitrogen and phosphorus in roughly 16:1 molar ratios based on Redfield proportions characterizing marine plankton biomass.

4.2 Stoichiometric Imbalances and Competition

Deviations from this balanced ratio create competitive advantages for organisms with flexible

nutrient requirements or specialized acquisition capabilities. When nitrogen loading exceeds phosphorus, high N:P ratios develop that favor organisms with low phosphorus demands or efficient phosphorus storage mechanisms (Klausmeier et al., 2004). Conversely, low N:P ratios from phosphorus-rich pollution select for nitrogen-fixing cyanobacteria or species capable of surviving prolonged nitrogen starvation through luxury uptake and storage (Schindler et al., 2008).

Algal taxa differ substantially in their nutrient requirements and flexibility. Green algae and diatoms typically maintain relatively fixed cellular N:P ratios close to Redfield proportions. Cyanobacteria show greater stoichiometric flexibility, able to adjust cellular ratios across wider ranges by varying polyphosphate storage and protein content. This flexibility allows cyanobacteria to maintain growth under both high and low N:P conditions, partially explaining their dominance across diverse nutrient regimes.

4.3 Freshwater N:P Dynamics

Many freshwater systems receiving agricultural runoff maintain high N:P ratios because modern fertilizers contain substantial nitrogen relative to phosphorus. These conditions might seem unlikely to produce cyanobacterial blooms since nitrogen-fixing cyanobacteria theoretically should dominate only under nitrogen limitation. However, observations frequently show that cyanobacteria bloom in nitrogen-rich, high N:P waters, revealing that factors beyond simple nitrogen availability control their success (Dolman et al., 2012). This apparent paradox has generated considerable scientific debate about optimal nutrient management strategies. Some researchers initially interpreted high N:P ratios as indicating that phosphorus limits growth and therefore phosphorus reduction alone, should control blooms. Others argued that nitrogen remains important even at high N:P ratios because absolute nitrogen concentrations still influence growth rates and community composition.

4.4 Absolute Phosphorus Thresholds

Research has revealed that phosphorus loading magnitude matters more than N:P ratio for determining whether cyanobacteria dominate. When phosphorus concentrations exceed approximately 20 micrograms per liter, cyanobacteria commonly bloom regardless of nitrogen availability (Downing

et al., 2001). This finding suggests that absolute phosphorus supply sets a permissive condition for cyanobacterial dominance, while nitrogen availability influences which specific taxa occur within the cyanobacterial community (Havens et al., 2003).

In phosphorus-rich but nitrogen-poor systems, nitrogen-fixing genera like *Anabaena* and *Aphanizomenon* predominate, accessing atmospheric N₂ to supplement limited dissolved nitrogen. In systems rich in both nutrients, non-fixing cyanobacteria like *Microcystis* outcompete nitrogen fixers because they avoid the energetic costs of fixation (Paerl et al., 2011). This differential success pattern explains why both low and high N:P ratios can support cyanobacterial blooms, though dominated by different genera with contrasting nitrogen acquisition strategies.

4.5 Management Controversies and Resolution

The optimal N:P ratio for managing blooms remains contentious in some scientific and management circles. Some researchers have advocated reducing nitrogen inputs to create nitrogen limitation that suppresses non-fixing cyanobacteria (Conley et al., 2009). This approach assumes that nitrogen-fixing species either will not fill the nitrogen limitation void or will be less problematic than non-fixing forms. Others argue that reducing only nitrogen lowers the N:P ratio and promotes nitrogen-fixing species that may prove equally or more toxic than non-fixing forms (Scott and Marcarelli, 2012). *Anabaena* and *Cylindrospermopsis*, both nitrogen fixers produce potent hepatotoxins and neurotoxins that pose serious health risks. Shifting from *Microcystis* dominance to *Anabaena* dominance through nitrogen reduction alone would not necessarily improve water safety.

Most evidence now supports dual nutrient reduction strategies that lower both nitrogen and phosphorus to shift systems back toward nutrient limitation that prevents blooms altogether (Schindler et al., 2016). This approach acknowledges that both nutrients contribute to bloom development and that reducing only one may allow problematic species adapted to that nutrient regime to dominate. Dual reduction proves more expensive and politically challenging to implement but offers better prospects for achieving substantial water quality improvements.

4.6 Marine and Estuarine Patterns

Estuaries and coastal waters show different N:P dynamics than freshwater systems. Marine environments typically experience nitrogen limitation more strongly than freshwater because phosphorus availability from ocean water remains relatively high (Howarth and Marino, 2006). Upwelling brings phosphorus-rich deep water to surface layers, maintaining elevated phosphorus concentrations even when nitrogen becomes depleted through biological uptake.

Coastal eutrophication therefore often correlates more tightly with nitrogen loading than phosphorus (Rabalais et al., 2009). The hypoxic zones in the Gulf of Mexico and Chesapeake Bay demonstrate nitrogen's role in stimulating algal production that leads to oxygen depletion when the organic matter sinks and decomposes (Kemp et al., 2005). These dead zones expand during high-flow periods when riverine nitrogen delivery peaks, then contract during low-flow periods, demonstrating the direct connection between nitrogen inputs and ecological impacts.

V. NITROGEN IMPACTS ON ALGAL TOXIN PRODUCTION

5.1 Beyond Biomass: The Toxicity Factor

Beyond influencing bloom magnitude, nitrogen availability affects the toxicity of individual algal cells through complex physiological mechanisms. This means that the public health threat from blooms depends not just on cell density but also on cellular toxin content, which varies with nitrogen supply conditions (Scott et al., 2013). Understanding these relationships proves critical for predicting when blooms pose greatest risks and for designing management interventions that reduce toxicity along with biomass.

5.2 Cyanobacterial Microcystins

Cyanobacterial microcystins represent the most widespread freshwater algal toxins, detected in bloom samples from every continent except Antarctica. These cyclic peptides function as chemical defenses against grazing zooplankton while also potentially serving metabolic roles within cells (Meissner et al., 2013). Microcystin production shows complicated responses to nitrogen availability that vary among strains and environmental contexts. Some studies find increased microcystin content

under nitrogen limitation, interpreted as a stress response where cells divert metabolism toward defense compound production when growth slows (Horst et al., 2014). Other studies report higher toxin production under nitrogen-replete conditions, suggesting that toxin synthesis requires adequate nitrogen supply for the peptide structure. These apparently contradictory findings likely reflect differences in experimental design, strain-specific responses, and the specific nitrogen concentrations tested.

5.3 Nitrogen Source Effects on Toxicity

Recent research suggests that the nitrogen source influences microcystin production more than total nitrogen concentration. Experiments with *Microcystis aeruginosa* demonstrate higher toxin production when cultured with nitrate compared to ammonium or urea (Harke and Gobler, 2013). This finding implies that agricultural runoff dominated by nitrate may promote more toxic blooms than sewage effluent rich in ammonium, even if total nitrogen loading remains equivalent.

The mechanistic basis for this response, likely involves regulatory connections between nitrate assimilation pathways and toxin biosynthesis genes (Steffen et al., 2014). Nitrate reduction requires expression of genes, encoding nitrate reductase and nitrite reductase enzymes. These genes are regulated by transcription factors that also influence expression of microcystin synthetase gene clusters. When cells activate nitrate reduction machinery, co-regulation may simultaneously upregulate toxin production, creating the observed source-specific effect.

5.4 Temporal Nitrogen Fluctuations

The timing of nitrogen availability also matters for cyanotoxin production. When *Microcystis* populations experience nitrogen starvation followed by nitrogen resupply, cellular microcystin can increase dramatically during the recovery phase (Pimentel and Giani, 2014). This pattern suggests that fluctuating nitrogen creates more toxic blooms than stable supply at equivalent average concentrations.

In systems with pulsed agricultural runoff, cyanobacteria may undergo repeated starvation-recovery cycles that elevate toxicity compared to steadily enriched conditions (Gobler et al., 2016). Cells experiencing nitrogen limitation accumulate

carbohydrates and lipids while reducing protein synthesis. When nitrogen becomes available again, rapid protein synthesis for growth may trigger compensatory increases in nitrogen-rich compounds including microcystins. This physiological response to fluctuating supply creates temporal variability in bloom toxicity that complicates risk assessment and management.

5.5 Dinoflagellate Saxitoxins

Saxitoxins produced by dinoflagellates show similarly complex nitrogen dependencies. The paralytic shellfish poisoning organism *Alexandrium fundyense* increases saxitoxin content under moderate nitrogen limitation, with toxicity peaking at intermediate nitrogen concentrations (John and Flynn, 2000). Severe nitrogen starvation reduces toxin production, as cellular metabolism slows overall and protein synthesis capacity declines.

This biphasic response means that the relationship between nitrogen and toxicity is non-linear, complicating predictions about how load reduction will affect health risks (Brandenburg et al., 2018). Moderate nitrogen reduction might increase toxicity by creating mild stress conditions, while aggressive reduction could decrease toxicity by severely limiting growth. The optimal management strategy depends on which portion of the response curve the system currently occupies information often unavailable without detailed monitoring of cellular toxin quotas throughout bloom development.

5.6 Diatom Domoic Acid

Domoic acid production by *Pseudo-nitzschia* diatoms increases markedly under nitrogen or silicon limitation. When growth becomes nutrient-constrained, *Pseudo-nitzschia* cells divert metabolism toward domoic acid biosynthesis while reducing cell division rates (Lema et al., 2017). This creates a trade-off between growth and toxin production mediated by resource availability. Blooms developing in coastal upwelling regions sometimes experience episodic nitrogen depletion as phytoplankton rapidly consume nutrients brought to surface waters. This creates pulses of high toxicity following the initial bloom development phase (Trainer et al., 2012). Shellfish feeding on these toxic cells accumulate domoic acid to concentrations that cause amnesic shellfish poisoning in human consumers. This stress-induced toxin production presents management challenges because

nutrient reduction strategies intended to control blooms can initially worsen toxicity even while decreasing bloom size (Kudela et al., 2020).

5.7 Molecular Mechanisms

The cellular mechanisms linking nitrogen metabolism to toxin biosynthesis remain incompletely understood despite substantial research effort. Some toxins appear to function as nitrogen storage compounds that cells can metabolize when external nitrogen becomes scarce, providing an internal nitrogen reserve (Neilan et al., 2013). Others may regulate nitrogen assimilation pathways or protect nitrogen-fixing enzymes from oxidative damage generated during photosynthesis. The complex genetic regulation of toxin production involves transcription factors responsive to cellular nitrogen status, creating molecular links between nutrient availability and toxicity (Spoof and Catherine, 2017). In *Microcystis*, the *mcyA-J* gene cluster encoding microcystin synthetase enzymes shows expression patterns correlated with nitrogen availability and form. Understanding these regulatory networks could eventually enable genetic markers for predicting bloom toxicity based on environmental nitrogen conditions, improving early warning

systems for water supply managers.

VI. CLIMATE CHANGE INTERACTIONS WITH NITROGEN-DRIVEN BLOOMS

6.1 Converging Stressors

Climate change has great impacts on nitrogen dynamics in aquatic ecosystem (Vancelli and Michelin, 2024). Climate warming and altered precipitation patterns interact with nitrogen pollution to affect bloom frequency and severity through multiple pathways. Rising temperatures influence nitrogen cycling rates, algal growth physiology, and water column stratification in ways that generally favor bloom development (Paerl and Huisman, 2008). Understanding these climate-nitrogen interactions proves essential for predicting future water quality trajectories and designing resilient management strategies. Climate change affects nitrogen-driven blooms through five primary mechanisms. Temperature increases accelerate microbial metabolism and nutrient regeneration, intensified stratification reduces vertical mixing while accumulating nutrients at depth, and altered precipitation produces larger episodic nutrient pulses (Flavia et al, 2024).

Climate Change Effects on Nitrogen-Driven Blooms (Rohini et al, 2025, Wells et al, 2015, Costa et al, 2022)

Climate Factor	Direct Effect	Nitrogen Cycle Impact	Bloom Consequences
Temperature seasons, Increase advantage	Accelerated microbial Metabolism	Faster nutrient regeneration, increased internal loading	Extended bloom cyanobacteria
Intensified Stratification vertical Migration	Reduced vertical mixing	Surface nitrogen depletion deeper nutrient accumulation	Advantage to buoyant cyanobacteria with
Altered triggering Precipitation Drought magnitude Conditions	More intense rainfall events Reduced water volume	Larger episodic nutrient pulses	opportunistic bloom
Sea level rise bloom	Saltwater Intrusion	Altered denitrification rates,	Modified coastal
Changed nitrogen speciation Ocean Acidification	Low pH	Changed nitrogen uptake kinetics	Patterns Enhanced growth
of certain dinoflagellates			

6.2 Temperature Effects on Nitrogen Cycling

Warmer temperatures accelerate nitrogen transformation rates in sediments and water. Microbial processes including nitrification,

denitrification, and ammonification all increase with temperature following standard metabolic rate relationships (Veraart et al., 2011). Faster nutrient regeneration from organic matter means that internal

nitrogen loading increases even when external inputs remain constant.

This temperature effect can extend bloom seasons in temperate regions where warming allows cyanobacteria to maintain populations later into fall and begin growing earlier in spring. In tropical systems, year-round warm temperatures already support continuous growth, so further warming may intensify rather than extend bloom periods (Kosten et al., 2012). The net effect increases nitrogen availability through faster recycling while simultaneously enhancing algal growth rates, creating positive feedbacks that amplify bloom responses.

6.3 Direct Temperature Effects on Algae

Temperature directly affects algal growth rates and competitive outcomes through species-specific thermal performance curves. Cyanobacteria generally have higher optimal temperature ranges than eukaryotic phytoplankton, with many species growing fastest between 25 and 35°C (Carey et al., 2012). Diatoms and green algae typically show optimal growth at cooler temperatures around 15-25°C.

As lakes and coastal waters warm, cyanobacteria gain competitive advantages over diatoms and chlorophytes that dominate cooler conditions (Rigosi et al., 2014). This temperature-driven species shift means that the same nitrogen loading produces different algal communities as climates warm. Management strategies effective under current conditions may prove less successful as warming shifts competitive balances toward cyanobacterial dominance even without changes in nutrient loading (Visser et al., 2016).

6.4 Stratification Intensification

Stratification patterns change with warming, affecting nitrogen availability to surface phytoplankton. Stronger thermal stratification reduces mixing between nutrient-rich bottom waters and the euphotic zone where algae photosynthesize (Woolway and Merchant, 2019). Surface layers become increasingly isolated from deeper nutrient pools, potentially creating nitrogen limitation even while overall water body nitrogen concentrations increase. This intensified stratification can paradoxically create nitrogen limitation in surface waters of eutrophic systems, potentially reducing

bloom biomass (Trolle et al., 2011). However, buoyant cyanobacteria that regulate their vertical position through gas vesicle inflation and deflation can access deeper nitrogen while remaining in sufficient light for photosynthesis. This capability provides another competitive advantage for cyanobacteria under climate warming scenarios, partially offsetting any bloom suppression from increased stratification (Huisman et al., 2004).

6.5 Altered Precipitation Patterns

Altered precipitation regimes affect nitrogen delivery patterns to aquatic systems. More intense rainfall events typical of changing climate patterns flush greater nutrient pulses from watersheds during individual storm events (Michalak et al., 2013). The increasing frequency of heavy precipitation in many regions means that nitrogen loading becomes more episodic, with larger individual events separated by longer dry periods.

These pulsed inputs favor opportunistic bloom-forming species that can rapidly exploit nutrient availability (Paerl and Paul, 2012). Species with fast maximum growth rates and efficient nutrient uptake kinetics gain advantages over slower-growing competitors during these transient resource pulses. The timing of precipitation events relative to temperature and stratification patterns influences whether pulsed nutrients trigger blooms or get consumed by diverse phytoplankton assemblages before problematic densities develop (Pryor et al., 2009).

6.6 Drought Concentration Effects

Drought conditions concentrate nitrogen in reduced water volumes and slow flushing rates that would normally dilute and export nutrients. During droughts, lakes and reservoirs can experience dramatically elevated nitrogen concentrations from the same absolute loading that would produce lower concentrations under wetter conditions (Mosley, 2015).

The combination of high nutrients, warm temperatures, and stable stratification during droughts creates conditions particularly favorable for intense cyanobacterial blooms (Bonilla et al., 2016). Extended droughts also reduce groundwater levels, potentially mobilizing legacy nitrogen stored in aquifer sediments and delivering it to surface waters when flow resumes. Climate projections suggest

increasing drought frequency and severity in many regions, implying that concentration effects will become more important drivers of bloom dynamics.

6.7 Sea Level Rise and Coastal Impacts

Sea level rise and saltwater intrusion into coastal freshwater systems alter nitrogen dynamics through multiple mechanisms. Increased salinity affects nitrogen speciation and microbial transformation rates in ways that can either enhance or reduce nitrogen availability depending on specific conditions (Herbert et al., 2015). Coastal wetlands that naturally remove nitrogen through denitrification may lose this function as saltwater inundation changes soil chemistry and plant communities.

Sulfate in seawater inhibits methane production but can also affect nitrogen cycling through sulfate-reducing bacteria that compete with denitrifiers for organic carbon (Neubauer, 2013). The net effect on nitrogen loading to estuaries and near-shore waters likely increases as saltwater intrusion compromises natural nitrogen removal processes in coastal watersheds (Tully et al., 2019). This adds to direct nitrogen pollution from human activities, creating combined pressures on coastal water quality.

6.8 Ocean Acidification

Ocean acidification from increased atmospheric CO₂ dissolution may influence nitrogen-limited marine blooms through altered phytoplankton physiology. Lower pH affects the chemical speciation of nitrogen and can alter phytoplankton nitrogen uptake kinetics by changing the energetics of transport across cell membranes (Hutchins et al., 2009).

Some bloom-forming dinoflagellates show enhanced growth under acidified conditions, potentially because increased CO₂ availability for photosynthesis allows them to allocate more resources to nitrogen acquisition (Fu et al., 2008). The combined effects of warming, acidification, and nitrogen pollution create novel environmental conditions that may favor HAB species over historically dominant phytoplankton (Wells et al., 2020). Understanding these interactions requires integrated research approaches examining multiple stressors simultaneously rather than studying each factor in isolation.

VII. MANAGEMENT IMPLICATIONS AND STRATEGIES

7.1 The Challenge of Implementation

Controlling nitrogen inputs represents the most direct approach to preventing blooms, yet implementing effective reduction strategies faces substantial political, economic, and technical challenges. Agricultural operations generate the majority of nitrogen pollution in many watersheds, but farm-level changes require cooperation from numerous independent operators with varying economic constraints and technical capacities (Carpenter et al., 1998). Point sources like wastewater treatment plants are easier to regulate through permit systems, yet still require expensive infrastructure upgrades to achieve meaningful load reductions (Withers et al., 2014).

7.2 Agricultural Best Management Practices

Agricultural nitrogen management strategies include reducing fertilizer application rates to match crop requirements more precisely, timing applications to minimize runoff losses, and creating buffer zones that intercept nutrients before they reach streams. Precision agriculture technologies GPS-guided variable rate application, soil sensors, plant tissue testing, allow farmers to apply nitrogen only where and when crops can use it efficiently (Sharpley et al., 2013).

Cover crops planted during fallow periods take up soil nitrogen that would otherwise wash away during winter and spring precipitation events. Species like cereal rye and winter wheat establish quickly in fall, survive winter dormancy, and resume growth in early spring before cash crop planting (Tonitto et al., 2006). These cover crops can capture 30-50 pounds of nitrogen per acre that would otherwise leach to groundwater or run off to surface waters.

Controlled drainage systems in tile-drained fields retain water and nutrients on farm fields rather than rapidly exporting them to streams. Structures installed in drainage outlets allow farmers to manage water table levels seasonally, holding water during periods when crops are not actively growing and draining fields when planting or harvesting requires dry conditions (Skaggs et al., 2012). These practices can reduce nitrogen losses by 20-50% when properly implemented, though adoption rates remain limited by economic considerations, technical complexity, and farm-specific constraints (Liu et al., 2017).

7.3 Wetland Restoration and Construction

Wetland restoration and construction provides natural nitrogen removal through denitrification processes that convert nitrate to nitrogen gas. Wetlands positioned to intercept agricultural drainage can remove substantial nitrogen loads before water reaches lakes or estuaries (Mitsch et al., 2001). Denitrifying bacteria in wetland soils use nitrate as an electron acceptor during organic matter decomposition under anaerobic conditions, releasing N₂ gas to the atmosphere.

The Mississippi River Basin has identified wetland restoration as a key strategy for reducing nitrogen delivery to the Gulf of Mexico hypoxic zone (Dale et al., 2010). Models suggest that restoring millions of acres of wetlands in strategic locations could reduce nitrogen loads by 20-40%, substantially shrinking the dead zone. However, wetlands require land area and sustained hydrology, creating implementation barriers in intensively farmed landscapes where land values are high and drainage infrastructure is deeply entrenched (Crumpton et al., 2006).

7.4 Advanced Wastewater Treatment

Wastewater treatment technology has advanced to achieve much greater nitrogen removal than conventional secondary treatment that primarily removes organic matter and solids. Biological nutrient removal (BNR) processes use sequential aerobic and anoxic conditions to allow bacteria to nitrify ammonium to nitrate under oxygen-rich conditions, then denitrify nitrate to nitrogen gas under oxygen-poor conditions (Grady et al., 2011).

Advanced BNR facilities can reduce effluent nitrogen concentrations, to below 3 milligrams per liter compared to 15-30 milligrams per liter, from conventional secondary treatment (Pehlivanoglu-Mantas and Sedlak, 2008). Some facilities achieve even lower concentrations below 1 mg/L, through enhanced treatment processes. Widespread adoption of these technologies would substantially reduce point source loading, but requires significant capital investment that many municipalities struggle to finance through rate increases or bond measures (Carey and Migliaccio, 2009).

7.5 Targeted Load Reduction Strategies

Targeted load reduction based on ecological understanding of nitrogen-bloom relationships may prove more efficient than across-the-board cuts that

treat all nitrogen inputs equally. If ammonium proves more problematic than nitrate for stimulating toxic cyanobacteria in a particular system, prioritizing wastewater treatment upgrades over agricultural nitrate reduction would make sense (Glibert et al., 2016).

If spring nitrate pulses trigger benign diatom blooms while summer nitrogen promotes toxic cyanobacteria, seasonal load restrictions might target warm-season inputs specifically (Harris et al., 2014). This could involve storing agricultural runoff in constructed wetlands or retention ponds during spring, then releasing it slowly during summer when crop uptake rates are highest. Such targeted approaches require detailed understanding of system-specific nitrogen-bloom relationships but potentially achieve better outcomes with lower overall costs than untargeted reduction strategies.

7.6 Adaptive Management Frameworks

Adaptive management approaches that monitor bloom responses to load reduction can optimize strategies over time through iterative learning. Given uncertainty about how specific systems will respond to changed nitrogen inputs, implementing reductions while carefully tracking water quality outcomes allows adjustment of management actions based on observed responses (Hallegraeff et al., 2017).

This learning-by-doing approach acknowledges the complexity of nitrogen-bloom relationships while making progress toward improved conditions rather than delaying action until perfect understanding is achieved (Stow et al., 2015). Adaptive management requires sustained monitoring programs, willingness to adjust strategies when initial approaches prove ineffective, and organizational structures that can respond flexibly to new information. These requirements challenge traditional regulatory frameworks that prefer fixed standards and unchanging management prescriptions.

7.7 Recovery Timelines and Stakeholder Expectations

Recovery timelines remain problematic for maintaining political support through extended improvement periods. Some systems require decades of load reduction before water quality improves substantially due to legacy nutrients stored in sediments (Jeppesen et al., 2005). Internal loading from sediments can sustain blooms for 10-30 years

after external loads decrease, creating a lag between management actions and ecosystem responses.

Setting realistic expectations for recovery timelines prevents stakeholders from abandoning effective strategies prematurely when rapid improvement fails to materialize (Meals et al., 2010). Long-term monitoring programs that document gradual trends prove essential for sustaining commitment through extended recovery periods. Communicating partial successes, reduced bloom frequency, shorter bloom duration, lower toxin concentrations, helps maintain support even when dramatic visual improvements remain distant (Schindler et al., 2016).

VIII. SYNTHESIS AND FUTURE RESEARCH DIRECTIONS

8.1 Key Findings Integration

Nitrogen pollution drives harmful algal bloom development through multiple interacting mechanisms that vary among ecosystem types, seasons, and species assemblages. Excessive nitrogen inputs from agricultural runoff and wastewater discharge provide raw material for rapid algal growth that overwhelms natural system capacity to assimilate nutrients without problematic biomass accumulation. Different nitrogen forms, nitrate, ammonium, organic compounds, favor distinct algal groups through taxon-specific uptake capabilities and competitive advantages. Temporal dynamics of nitrogen delivery determine whether systems experience episodic blooms following nutrient pulses or sustained blooms from chronic enrichment. Interactions between nitrogen and phosphorus create complex co-limitation scenarios where both absolute concentrations and nutrient ratios influence competitive outcomes. Climate change intensifies nitrogen-driven bloom problems through warming that favors cyanobacteria, altered precipitation that creates larger episodic nutrient pulses, and strengthened stratification that advantages buoyant species. Nitrogen availability influences not just bloom magnitude but also cellular toxicity through stress responses and metabolic regulation of toxin biosynthesis pathways. This dual effect means bloom management must address both population size and toxin content, objectives that may conflict under certain reduction strategies where moderate nutrient limitation increases cellular toxicity while decreasing total biomass (Dogharam 2024)

8.2 Management Synthesis

Effective bloom management requires reducing nitrogen loads through agricultural best management practices, wetland restoration, and advanced wastewater treatment implemented in coordinated watershed-scale programs. Understanding how different nitrogen forms and temporal patterns affect specific bloom types allows targeted reduction strategies potentially more efficient than uniform cuts treating all nitrogen inputs identically. The slow recovery of systems with legacy sediment nutrients demands sustained commitment to load reduction over decades, timelines that challenge political systems oriented toward short-term results and rapid returns on investment. Adaptive management frameworks that monitor responses and adjust strategies based on observed outcomes provide pathways for progress despite incomplete understanding of complex nitrogen-bloom relationships (Christiana et al, 2012)

8.3 Critical Knowledge Gaps

Several critical knowledge gaps limit prediction and management capabilities. The effects of novel anthropogenic organic nitrogen compounds on bloom dynamics remain poorly characterized. Herbicide metabolites, pharmaceutical residues, and industrial byproducts increasingly dominate dissolved organic nitrogen pools in urbanized watersheds, but their bioavailability and effects on species composition are largely unknown.

Molecular mechanisms linking nitrogen metabolism to toxin production require further elucidation to enable predictive models of bloom toxicity based on environmental nitrogen conditions. Current understanding allows only crude predictions that moderate nitrogen limitation often increases toxicity, but cannot specify optimal reduction targets that minimize both biomass and toxin concentrations simultaneously.

Climate change interactions with nitrogen pollution will modify bloom dynamics in ways models capture imperfectly. Multi-stressor experiments examining combined effects of warming, altered precipitation patterns, increased CO₂, and varying nitrogen loads are needed to develop robust projections of future bloom risks. Most existing research examines single stressors or pairs of factors, potentially missing important interactive effects that emerge only when multiple stressors operate

simultaneously.

8.4 Emerging Research Frontiers

Emerging research frontiers include application of molecular techniques for bloom prediction and early warning. Environmental DNA and RNA analysis can detect bloom-forming species before they reach visible densities, potentially enabling preventive interventions (Chorus and Welker, 2021). Quantifying expression of toxin biosynthesis genes could provide early indicators of developing toxicity before cell concentrations reach dangerous levels.

Remote sensing technologies offer capabilities for monitoring blooms at scales and frequencies impossible with traditional sampling approaches. Satellite imagery can track bloom extent, duration, and movement patterns across entire water bodies or coastal regions (Anderson et al., 2021). Developing algorithms that relate spectral signatures to nitrogen concentrations and algal toxicity would enhance management capabilities substantially.

8.5 Concluding Perspective

Nitrogen-driven harmful algal blooms represent complex environmental problems requiring coordinated responses across multiple scales from individual farms to entire watersheds, from immediate interventions to decades-long commitments, from technical solutions to policy reforms. The science has advanced substantially over recent decades, moving from simple recognition that nutrients cause blooms to nuanced understanding of how specific nitrogen forms, temporal patterns, and environmental interactions influence bloom development and toxicity.

This improved understanding must now translate into effective management actions that reduce nitrogen pollution and protect aquatic ecosystems. The technical knowledge exists; implementation requires sustained political will, adequate funding, and coordinated action across jurisdictional boundaries and stakeholder groups with diverse interests. The alternative, continued degradation of freshwater and marine ecosystems, imposes costs that far exceed those required for effective nitrogen management through diminished ecosystem services, increased water treatment expenses, and public health impacts that already affect millions globally.

REFERENCES

- [1] Anderson, D.M., Alpermann, T.J., Cembella, A.D., Collos, Y., Masseret, E., and Montresor, M. (2012). The globally distributed genus *Alexandrium*: multifaceted roles in marine ecosystems and impacts on human health. *Harmful Algae*, 14, 10-35.
- [2] Anderson, D.M., Fensin, E., Gobler, C.J., Hoeglund, A.E., Hubbard, K.A., Kulis, D.M., Landsberg, J.H., Lefebvre, K.A., Provoost, P., Richlen, M.L., Smith, J.L., Solow, A.R., and Trainer, V.L. (2021). Marine harmful algal blooms (HABs) in the United States: history, current status and future trends. *Harmful Algae*, 102, 101975.
- [3] Beusen, A.H.W., Doelman, J.C., Van Beek, L.P.H., Van Puijenbroek, P.J.T.M., Mogollón, J.M., Van Grinsven, H.J.M., Stehfest, E., Van Vuuren, D.P., and Bouwman, A.F. (2022). Exploring river nitrogen and phosphorus loading and export to global coastal waters in the Shared Socio-economic pathways. *Global Environmental Change*, 72, 102426.
- [4] Beversdorf, L.J., Miller, T.R., and McMahon, K.D. (2013). The role of nitrogen fixation in cyanobacterial bloom toxicity in a temperate, eutrophic lake. *PLoS ONE*, 8, e56103.
- [5] Bonilla, S., Aubriot, L., Soares, M.C.S., González-Piana, M., Fabre, A., Huszar, V.L., Lüring, M., Antoniadou, D., Padisák, J., and Kruk, C. (2012). What drives the distribution of the bloom-forming cyanobacteria *Planktothrix agardhii* and *Cylindrospermopsis raciborskii*? *FEMS Microbiology Ecology*, 79, 594-607.
- [6] Karem M Brandenburg¹, Sylke Wohlrab^{2,3}, Uwe John^{2,3}, Anke Kremp⁴, Jacqueline Jerney⁴, Bernd Krock², and Van de Waal¹. (2018). Intraspecific trait variation and trade-offs within and across populations of a toxic dinoflagellate. *Ecology Letters*, 21, 1561-1571.
- [7] Bronk, D.A., See, J.H., Bradley, P., and Killberg, L. (2007). DON as a source of bioavailable nitrogen for phytoplankton. *Biogeosciences*, 4, 283-296.
- [8] Carey, R.O. and Migliaccio, K.W. (2009). Contribution of wastewater treatment plant effluents to nutrient dynamics in aquatic systems: a review. *Environmental Management*, 44, 205-217.
- [9] Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith,

- V.H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications*, 8, 559-568.
- [10] Collos, Y., Gagne, C., Laabir, M., Vaquer, A., Cecchi, P., and Souchu, P. (2004). Nitrogenous nutrition of *Alexandrium catenella* (Dinophyceae) in cultures and in Thau lagoon, southern France. *Journal of Phycology*, 40, 96-103.
- [11] Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C., and Likens, G.E. (2009). Controlling eutrophication: nitrogen and phosphorus. *Science*, 323, 1014-1015.
- [12] Costa, Diogo & Sutter, Caleb & Shepherd, Anita & Jarvie, Helen & Wilson, Henry & Elliott, Jane & Liu, Jian & Macrae, Merrin. (2022). Impact of climate change on catchment nutrient dynamics: insights from around the world. *Environmental Reviews*. 31. 10.1139/er-2021-0109.
- [13] Crumpton, W.G., Stenback, G.A., Fisher, S.W., Stenback, J.Z., and Green, D.I. (2006). Water quality performance of wetlands receiving nonpoint-source nitrogen loads: nitrate and total nitrogen removal efficiency and controlling factors. *Journal of Environmental Quality*, 45, 1-13.
- [14] Dai, M., Luo, Y., Achterberg, E.P., Browning, T.J., Cai, Y., Cao, Z., Chai, F., Chen, B., Church, M.J., Ci, D., Du, C., et al. (2023). Upper ocean biogeochemistry of the oligotrophic North Pacific Subtropical Gyre: from nutrient sources to carbon export. *Reviews of Geophysics*, 59, e2020RG000720.
- [15] Dolman, A.M., Rucker, J., Pick, F.R., Fastner, J., Rohrlack, T., Mischke, U., and Wiedner, C. (2012). Cyanobacteria and cyanotoxins: the influence of nitrogen versus phosphorus. *PLoS ONE*, 7, e38757
- [16] Dorgham, Mohamed. (2014). Effects of Eutrophication. 10.1007/978-94-007-7814-63.
- [17] Downing, J.A., Watson, S.B., and McCauley, E. (2001). Predicting cyanobacteria dominance in lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 58, 1905-1908.
- [18] Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., and Smith, J.E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10, 1135-1142.
- [19] Flavia Dory, Veronica Nava, Morena Spreafico, Valentina Orlandi, Valentina Soler, Barbara Leoni. Interaction between temperature and nutrients: How does the phytoplankton community cope with the climate change. *Science of the total environment*, 906(2024) 167566
- [20] Finlay, K., Patoine, A., Donald, D.B., Bogard, M.J., and Leavitt, P.R. (2010). Experimental evidence that pollution with urea can degrade water quality in phosphorus-rich lakes of the Northern Great Plains. *Limnology and Oceanography*, 55, 1213-1230.
- [21] Flores, E. and Herrero, A. (2005). Nitrogen assimilation and nitrogen control in cyanobacteria. *Biochemical Society Transactions*, 33, 164-167.
- [22] Flynn, K.J., Stoecker, D.K., Mitra, A., Raven, J.A., Glibert, P.M., Hansen, P.J., Granéli, E., and Burkholder, J.M. (2013). Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. *Journal of Plankton Research*, 35, 3-11.
- [23] Flynn, K.J., Mitra, A., Anestis, K., Anschutz, A.A., Calbet, A., Ferreira, G.D., Gypens, N., Hansen, P.J., John, U., Martin, J.L., Mansour, J.S., et al. (2022). Mixotrophic protists and a new paradigm for marine ecology: where does plankton research go now? *Journal of Plankton Research*, 41, 375-391.
- [24] Fu, F.X., Warner, M.E., Zhang, Y., Feng, Y., and Hutchins, D.A. (2008). Effects of increased temperature and CO₂ on photosynthesis, growth, and elemental ratios in marine *Synechococcus* and *Prochlorococcus* (Cyanobacteria). *Journal of Phycology*, 43, 485-496.
- [25] Glibert, P.M. (2016). Margalef revisited: a new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. *Harmful Algae*, 55, 25-30.
- [26] Glibert, P.M. (2020). Harmful algae at the complex nexus of eutrophication and climate change. *Harmful Algae*, 91, 101583.
- [27] Glibert, P.M., Wilkerson, F.P., Dugdale, R.C., Raven, J.A., Dupont, C.L., Leavitt, P.R., Parker, A.E., Burkholder, J.M., and Kana, T.M.

- (2016). Pluses and minuses of ammonium and nitrate uptake and assimilation by phytoplankton and implications for productivity and community composition, with emphasis on nitrogen-enriched conditions. *Limnology and Oceanography*, 61, 165-197.
- [28] Glibert, P.M., Heil, C.A., Holligan, P.M., Revilla, M., Hoare, A., Alexander, J., and Mitra, A. (2022). Evidence for dissolved organic nitrogen and phosphorus uptake during a cyanobacterial bloom in Florida Bay. *Marine Ecology Progress Series*, 280, 73-83.
- [29] Gobler, C.J., Burkholder, J.M., Davis, T.W., Harke, M.J., Johengen, T., Stow, C.A., and Van de Waal, D.B. (2016). The dual role of nitrogen supplies in controlling the growth and toxicity of cyanobacterial blooms. *Harmful Algae*, 54, 87-97.
- [30] Granéli, E. and Hansen, P.J. (2006). Allelopathy in harmful algae: a mechanism to compete for resources In: *Ecology of Harmful Algae* (Granéli, E. and Turner, J.T., eds.), pp. 189-201. Springer, Berlin.
- [31] Hallegraeff, G.M., Anderson, D.M., Belin, C., Bottein, M.Y.D., Bresnan, E., Chinain, M., Enevoldsen, H., Iwataki, M., Karlson, B., McKenzie, C.H., Sunesen, I., et al. (2021). Perceived global increase in algal blooms is attributable to intensified monitoring and emerging bloom impacts. *Communications Earth & Environment*, 2, 178.
- [32] Justina J. Hampel ^{1,2*}, Mark J. McCarthy ², Sanni L Aalto ³, and Silvia E Newel³. (2020). Hurricane disturbance stimulated nitrification and altered ammonia oxidizer community structure in Lake Okeechobee and St. Lucie Estuary (Florida). *Frontiers in Microbiology*, 10, 2541.
- [33] Harke, M.J. and Gobler, C.J. (2013). Global transcriptional responses of the toxic cyanobacterium, *Microcystis aeruginosa*, to nitrogen stress, phosphorus stress, and growth on organic matter. *PLoS ONE*, 8, 69834.
- [34] Harke, M.J., Steffen, M.M., Gobler, C.J., Otten, T.G., Wilhelm, S.W., Wood, S.A., and Paerl, H.W. (2016). A review of the global ecology, genomics, and biogeography of the toxic cyanobacterium, *Microcystis* spp. *Harmful Algae*, 54, 4-20.
- [35] K.E Havens ¹, T. Fukushima, Xie, P., T. Iwakuma, R.T., James, N. Takamura, T. Hanazato, and, T. Yamamoto (2003). Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donghu (PR China), and Okeechobee (USA). *Environmental Pollution*, 111, 263-272.
- [36] Herbert, E.R., Boon, P., Burgin, A.J., Neubauer, S.C., Franklin, R.B., Ardón, M., Hopfensperger, K.N., Lamers, L.P.M., and Gell, P. (2015). A global perspective on wetland salinization: ecological consequences of a growing threat to freshwater wetlands. *Ecosphere*, 6, 1-43.
- [37] Geoffrey P Horst ¹, Orlando Sarnelle ², Jeffrey D White¹, Stephen K. Hamilton ³, Rajreni B Kaul ¹, and Juliana D Bressie ⁴. (2014). Nitrogen availability increases the toxin quota of a harmful cyanobacterium, *Microcystis aeruginosa*. *Water Research*, 54, 188-198.
- [38] Howarth, R.W. and Marino, R. (2006). Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. *Limnology and Oceanography*, 51, 364-376.
- [39] Huisman, J., Codd G.A., Paerl, H.W., Ibelings, B.W., Verspagen, J.M.H., and Visser, P.M. (2018). Cyanobacterial blooms. *Nature Reviews Microbiology*, 16, 471-483.
- [40] Huisman, J., Sharples, J., Stroom, J.M., Visser, P.M., Kardinaal, W.E.A., Verspagen, J.M.H., and Sommeijer, B. (2004). Changes in turbulent mixing shift competition for light between phytoplankton species. *Ecology*, 85, 2960-2970.
- [41] Hutchins, D.A., Mulholland, M.R., and Fu, F. (2009). Nutrient cycles and marine microbes in a CO₂-enriched ocean. *Oceanography*, 22, 128-145.
- [42] Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B., Gerdeaux, D., et al. (2005). Lake responses to reduced nutrient loading an analysis of contemporary long-term data from 35 case studies. *Freshwater Biology*, 50, 1747-1771.
- [43] John, E.H. and Flynn, K.J. (2010). Growth dynamics and toxicity of *Alexandrium fundyense* (Dinophyceae): the effect of changing N:P supply ratios on internal toxin and nutrient levels. *European Journal of Phycology*, 35, 11-23.
- [44] Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G.,

- Cornwell, J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., et al. (2005). Eutrophication of Chesapeake Bay: historical trends and ecological interactions. *Marine Ecology Progress Series*, 303, 1-29.
- [45] Klausmeier, C.A., Litchman, E., Daufresne, T., and Levin, S.A. (2004). Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature*, 429, 171-174.
- [46] Kosten, S., Huszar, V.L., Bécares, E., Costa, L.S., van Donk, E., Hansson, L.A., Jeppesen, E., Kruk, C., Lacerot, G., Mazzeo, N., De Meester, L., et al. (2012). Warmer climates boost cyanobacterial dominance in shallow lakes. *Global Change Biology*, 18, 118-126.
- [47] Kudela, R.M., Lane, J.Q., and Cochlan, W.P. (2008). The potential role of anthropogenically derived nitrogen in the growth of harmful algae in California, USA. *Harmful Algae*, 8, 103-110.
- [48] Kimberly ALema¹, Maria Latimier², Elisabeth Nézan³, Juliette Fauchot⁴, and Michael Le Gac, M. (2017). Inter and intra-specific growth and domoic acid production in relation to nutrient ratios and concentrations in *Pseudo-nitzschia*: phosphate an important factor. *Harmful Algae*, 64, 11-19.
- [49] Li, M., Glibert, P.M., and Gao, Y. (2023). Spatial and temporal dynamics of dissolved inorganic nitrogen in the Chesapeake Bay: a 30-year analysis. *Science of the Total Environment*, 858, 159774.
- [50] Liu, J., Ulén, B., Bergström, L., and Aronsson, H. (2017). Potential phosphorus release from catch crop shoots and roots after freezing-thawing. *Plant and Soil*, 371, 543-557.
- [51] Lomas, M.W. and Glibert, P.M. (1999). Interactions between NH_4^+ and NO_3^- uptake and assimilation: comparison of diatoms and dinoflagellates at several growth temperatures. *Marine Biology*, 133, 541-551.
- [52] Meals, D.W., Dressing, S.A., and Davenport, T.E. (2010). Lag time in water quality response to best management practices: a review. *Journal of Environmental Quality*, 39, 85-96.
- [53] Meissner, S., Fastner, J., and Dittmann, E. (2013). Microcystin production revisited: conjugate formation makes a major contribution. *Environmental Microbiology*, 15, 1810-1820.
- [54] Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., Chaffin, J.D., Cho, K., Confesor, R., Daloglu, I., DePinto, J.V., et al. (2013). Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proceedings of the National Academy of Sciences*, 110, 6448-6452.
- [55] Mitsch, W.J., Day, J.W., Gilliam, J.W., Groffman, P.M., Hey, D.L., Randall, G.W., and Wang, N. (2001). Reducing nitrogen loading to the Gulf of Mexico from the Mississippi River Basin: strategies to counter a persistent ecological problem. *BioScience*, 51, 373-388.
- [56] Mosley, L.M. (2015). Drought impacts on the water quality of freshwater systems; review and integration. *Earth-Science Reviews*, 140, 203-214.
- [57] Neilan, B.A., Pearson, L.A., Muenchhoff, J., Moffitt, M.C., and Dittmann, E. (2013). Environmental conditions that influence toxin biosynthesis in cyanobacteria. *Environmental Microbiology*, 15, 1239-1253.
- [58] Neubauer, S.C. (2013). Ecosystem responses of a tidal freshwater marsh experiencing saltwater intrusion and altered hydrology. *Estuaries and Coasts*, 36, 491-507.
- [59] Paerl, H.W. and Huisman, J. (2008). Blooms like it hot. *Science*, 320, 57-58.
- [60] Paerl, H.W. and Otten, T.G. (2013). Harmful cyanobacterial blooms: causes, consequences, and controls. *Microbial Ecology*, 65, 995-1010.
- [61] Paerl, H.W. and Paul, V.J. (2012). Climate change: links to global expansion of harmful cyanobacteria. *Water Research*, 46, 1349-1363.
- [62] Paerl, H.W., Fulton, R.S., Moisaner, P.H., and Dyble, J. (2001). Harmful freshwater algal blooms, with an emphasis on cyanobacteria. *The Scientific World JOURNAL*, 1, 76-113.
- [63] Paerl, H.W., Dennis, R.L., and Whittall, D.R. (2006). Atmospheric deposition of nitrogen: implications for nutrient over-enrichment of coastal waters. *Estuaries and Coasts*, 25, 677-693.
- [64] Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y., and Gardner, W.S. (2011). Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): the need for a dual nutrient (N & P) management strategy. *Water Research*, 45, 1973-1983.
- [65] Paerl, H.W., Hall, N.S., and Calandrino, E.S. (2016). Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. *Science of the Total Environment*, 409, 1739-1745.

- [66] Hans.W. Paerl, Gardner, W.S., Havens, K.E., Joyner, A.R., McCarthy, M.J., Newell, S.E., Qin, B., and Scott, J.T. (2020). Mitigating cyanobacterial harmful algal blooms in aquatic ecosystems impacted by climate change and anthropogenic nutrients. *Harmful Algae*, 54, 213-222.
- [67] Elif Pehlivanoglu-Mantas, and David L Sedlak, (2008). Measurement of dissolved organic nitrogen forms in wastewater effluents: concentrations, size distribution and NDMA formation potential. *Water Research*, 42, 3890-3898.
- [68] Juliana S.M. Pimentel and Alesander Giani, . (2014). Microcystin production and regulation under nutrient stress conditions in toxic *Microcystis* strains. *Applied and Environmental Microbiology*, 80, 5836-5843.
- [69] Pryor, S.C., Howe, J.A., and Kunkel, K.E. (2009). How spatially coherent and statistically robust are temporal changes in extreme precipitation in the contiguous USA? *International Journal of Climatology*, 29, 31-45.
- [70] Rabalais, N.N., Diaz, R.J., Levin, L.A., Turner, R.E., Gilbert, D., and Zhang, J. (2009). Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences*, 7, 585-619.
- [71] Reichwaldt, E.S. and Ghadouani, A. (2012). Effects of rainfall patterns on toxic cyanobacterial blooms in a changing climate: between simplistic scenarios and complex dynamics. *Water Research*, 46, 1372-1393.
- [72] Reynolds, C.S. (2006). *The Ecology of Phytoplankton*. Cambridge University Press, Cambridge.
- [73] Rigosi, A., Carey, C.C., Ibelings, B.W., and Brookes, J.D. (2014). The interaction between climate warming and eutrophication to promote cyanobacteria is dependent on trophic state and varies among taxa. *Limnology and Oceanography*, 59, 99-114.
- [74] Rohini Mattoo*, Usman B. Mallikarjuna, and Naveenachar Hemachar. Ecosystem and climate change impacts on the nitrogen cycle and biodiversity. *Nitrogen*, 2025: 6(5), 78
- [75] Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., Beaty, K.G., Lyng, M., and Kasian, S.E.M. (2008). Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proceedings of the National Academy of Sciences*, 105, 11254-11258.
- [76] Schindler, D.W., Carpenter, S.R., Chapra, S.C., Hecky, R.E., and Orihel, D.M. (2016). Reducing phosphorus to curb lake eutrophication is a success. *Environmental Science & Technology*, 50, 8923-8929.
- [77] Scott, J.T. and Grantz, E.M. (2013). N₂ fixation exceeds internal nitrogen loading as a phytoplankton nutrient source in perpetually nitrogen-limited reservoirs. *Freshwater Science*, 32, 849-861.
- [78] Scott, J.T. and Marcarelli, A.M. (2012). Cyanobacteria in freshwater benthic environments. In: *Ecology of Cyanobacteria II*, pp. 271-289. Springer, Dordrecht.
- [79] Seitzinger, S.P., Sanders, R.W., and Styles, R. (2002). Bioavailability of DON from natural and anthropogenic sources to estuarine plankton. *Limnology and Oceanography*, 47, 353-366.
- [80] Seitzinger, S.P., Mayorga, E., Bouwman, A.F., Kroeze, C., Beusen, A.H.W., Billen, G., Van Drecht, G., Dumont, E., Fekete, B.M., Garnier, J., and Harrison, J.A. (2010). Global river nutrient export: a scenario analysis of past and future trends. *Global Biogeochemical Cycles*, 24, GB0A08.
- [81] Sharpley, A.N., Bergström, L., Aronsson, H., Bechmann, M., Bolster, C.H., Börling, K., Djodjic, F., Jarvie, H.P., Schoumans, O.F., Stamm, C., Tonderski, K.S., et al. (2013). Future agriculture with minimized phosphorus losses to waters: research needs and direction. *Ambio*, 44, 163-179.
- [82] Shatwell, T., Thiery, W., and Kirillin, G. (2019). Future projections of temperature and mixing regime of European temperate lakes. *Hydrology and Earth System Sciences*, 23, 1533-1551.
- [83] Smith, V.H. (2003). Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environmental Science and Pollution Research*, 10, 126-139.
- [84] Smith, J.M., Chavez, F.P., and Francis, C.A. (2014). Ammonium uptake by phytoplankton regulates nitrification in the sunlit ocean. *PLoS ONE*, 9, e108173.
- [85] Søndergaard, M., Jensen, J.P., and Jeppesen, E. (2003). Role of sediment and internal loading of phosphorus in shallow lakes. *Hydrobiologia*,

- 506, 135-145.
- [86] Sommer, U., Adrian, R., De Senerpont Domis, L., Elser, J.J., Gaedke, U., Ibelings, B., Jeppesen, E., Lürling, M., Molinero, J.C., Mooij, W.M., van Donk, E., and Winder, M. (2012). Beyond the Plankton Ecology Group (PEG) Model: Mechanisms driving plankton succession. *Annual Review of Ecology, Evolution, and Systematics*, 43, 429-448.
- [87] Spilling, K., Olli, K., Lehtoranta, J., Kremp, A., Tedesco, L., Tamelander, T., Klais, R., Peltonen, H., and Tamminen, T. (2018). Shifting diatom-dinoflagellate dominance during spring bloom in the Baltic Sea and its potential effects on biogeochemical cycling. *Frontiers in Marine Science*, 5, 327.
- [88] Steffen, M.M., Davis, T.W., McKay, R.M.L., Bullerjahn, G.S., Krausfeldt, L.E., Stough, J.M.A., Neitzey, M.L., Gilbert, N.E., Boyer, G.L., Johengen, T.H., Gossiaux, D.C., et al. (2017). Ecophysiological examination of the Lake Erie *Microcystis* bloom in 2014: linkages between biology and the water supply shutdown of Toledo, OH. *Environmental Science & Technology*, 51, 6745-6755.
- [89] Steffen, M.M., Belisle, B.S., Watson, S.B., Boyer, G.L., and Wilhelm, S.W. (2014). Status, causes and controls of cyanobacterial blooms in Lake Erie. *Journal of Great Lakes Research*, 40, 215-225.
- [90] Sterner, R.W. (2008). On the phosphorus limitation paradigm for lakes. *International Review of Hydrobiology*, 93, 433-445.
- [91] Stoecker, D.K. and Lavrentyev, P.J. (2018). Mixotrophic plankton in the polar seas: a pan-Arctic review. *Frontiers in Marine Science*, 5, 292.
- [92] Stow, C.A., Cha, Y., Johnson, L.T., Confesor, R., and Richards, R.P. (2015). Long-term and seasonal trend decomposition of Maumee River nutrient inputs to western Lake Erie. *Environmental Science & Technology*, 49, 3263-3986.
- [93] Terseleer, N., Bruggeman, J., Lancelot, C., and Gypens, N. (2014). Trait-based representation of diatom functional diversity in a plankton functional type model of the eutrophied southern North Sea. *Limnology and Oceanography*, 59, 1958-1972.
- [94] Tonitto, C., David, M.B., and Drinkwater, L.E. (2006). Replacing bare fallows with cover crops in fertilizer-intensive cropping systems: a meta-analysis of crop yield and N dynamics. *Agriculture, Ecosystems & Environment*, 112, 58-72.
- [95] Trainer, V.L., Bates, S.S., Lundholm, N., Thessen, A.E., Cochlan, W.P., Adams, N.G., and Trick, C.G. (2012). *Pseudo-nitzschia* physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. *Harmful Algae*, 14, 271-300.
- [96] Trainer, V.L., Moore, S.K., Hallegraeff, G., Kudela, R.M., Clement, A., Mardones, J.I., and Cochlan, W.P. (2020). Pelagic harmful algal blooms and climate change: lessons from nature's experiments with extremes. *Harmful Algae*, 91, 101591.
- [97] Trolle, D., Hamilton, D.P., Pilditch, C.A., Duggan, I.C., and Jeppesen, E. (2010). Predicting the effects of climate change on trophic status of three morphologically varying lakes: implications for lake restoration and management. *Environmental Modelling & Software*, 26, 354-370.
- [98] Tully, K., Gedan, K., Epanchin-Niell, R., Strong, A., Bernhardt, E.S., BenDor, T., Mitchell, M., Kominoski, J., Jordan, T.E., Neubauer, S.C., and Weston, N.B. (2019). The invisible flood: the chemistry, ecology, and social implications of coastal saltwater intrusion. *BioScience*, 69, 368-378.
- [99] Van Meter, K.J., Basu, N.B., and Van Cappellen, P. (2016). Two centuries of nitrogen dynamics: legacy sources and sinks in the Mississippi and Susquehanna River Basins. *Global Biogeochemical Cycles*, 31, 2-23.
- [100] Van Meter, K.J., Van Cappellen, P., and Basu, N.B. (2018). Legacy nitrogen may prevent achievement of water quality goals in the Gulf of Mexico. *Science*, 360, 427-430.
- [101] Veraart, A.J., de Klein, J.J.M., and Scheffer, M. (2011). Warming can boost denitrification disproportionately due to altered oxygen dynamics. *PLoS ONE*, 6, e18508.
- [102] Viancelli A, Michelon W. Climate Change and Nitrogen Dynamics: Challenges and Strategies for a sustainable Future. *Nitrogen*. 2024;5(3) : 688-701.
- [103] Visser, P.M., Verspagen, J.M.H., Sandrini, G., Stal, L.J., Matthijs, H.C.P., Davis, T.W., Paerl, H.W., and Huisman, J. (2016). How rising CO₂ and global warming may stimulate harmful cyanobacterial blooms. *Harmful Algae*, 54, 145-159.

- [104] Wells, M.L., Karlson, B., Wulff, A., Kudela, R., Trick, C., Asnaghi, V., Berdalet, E., Cochlan, W., Davidson, K., De Rijcke, M., Dutkiewicz, S., et al. (2020). Future HAB science: directions and challenges in a changing climate. *Harmful Algae*, 91, 101632.
- [105] Wells ML, Trainer VL, Smayda TJ, Karlson BS, Trick CG, Kudela RM, Ishikwa A, Bernard S, Wulff A, Anderson DM, Cochlan WP. (2015). Harmful algal blooms and climate change; Learning from the past and present to forecast the future. *harmful Algae*. 1(49): 68-93
- [106] Withers, P.J.A., Neal, C., Jarvie, H.P., and Doody, D.G. (2014). Agriculture and eutrophication: where do we go from here? *Sustainability*, 6, 5853-5875.
- [107] Woolway, R.I. and Merchant, C.J. (2019). Worldwide alteration of lake mixing regimes in response to climate change. *Nature Geoscience*, 12, 271-276.