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Aquatic Ecology REVIEW

A cross-system mechanistic framework for phytoplankton bloom life cycles across aquatic environments

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GRAPHICAL ABSTRACT



PUBLIC SUMMARY

- A unified life-cycle framework for phytoplankton blooms was developed.
- Five key stages were identified: recruitment, proliferation, persistence, decline, and fate.
- Shared and system-specific bloom mechanisms were compared across aquatic environments.
- The cryosphere was examined as a distinct case study of bloom dynamics under extreme conditions.
- The framework provides a basis for cross-system bloom prediction under environmental change.

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Phytoplankton blooms recur across lakes, reservoirs, rivers, coastal oceans, and cryospheric systems, with life cycles shaped by system-specific environmental drivers. This review synthesizes how five universal stages—recruitment, proliferation, persistence, decline, and fate—are expressed across systems, highlighting overlooked contrasts. Recruitment is temperature-driven in stratified lakes but governed by hydrodynamic relaxation in rivers and reservoirs. Proliferation is phosphorus-driven in freshwaters and iron-limited in offshore marine systems, where it can also trigger cysteine synthase-mediated neurotoxin production in diatoms. Persistence reflects more than physiological tolerance: bloom-associated microbiomes buffer nutrient supply and may harbor antibiotic resistance genes under warming. Decline is shaped by residence time: slow-retention systems favor viral lysis and internal recycling, whereas fast-flowing systems favor physical export. Bloom fate is reshaped by plastisphere-associated microbial interactions altering organic matter remineralization and carbon export efficiency. In cryospheric environments, blooms are governed by ice physics rather than liquid-water dynamics: recruitment follows ice-melt release, proliferation depends on light duration under meltwater stratification, decline is triggered by refreezing, and fate is amplified through ice-albedo feedbacks. Despite system-specific controls, bloom progression follows five generalized ecological laws: threshold activation, resource-retention optimization, feedback stabilization, disturbance-driven reset, and ecological legacy propagation. Critical gaps remain—quantitative stage-transition thresholds are poorly constrained, phytoplankton physiological plasticity is rarely incorporated into models, and no framework resolves all five stages across the land-sea continuum. Addressing these gaps require trait-based parameterization, high-frequency observational networks, and coupled lake-river-estuary-coastal forecasting models. This framework provides a mechanistic foundation for transferable bloom prediction under climate change and hydrological regulation.

INTRODUCTION

Phytoplankton blooms, encompassing harmful algal blooms (HABs), high-biomass hypoxic events, and cryospheric primary production, are among the most ecologically and societally significant phenomena in aquatic systems worldwide. Their frequency, intensity, and geographic extent are increasing under the combined influences of eutrophication and climate change.[1,2,3] Despite extensive research, bloom studies remain largely system-specific, focusing on lakes, reservoirs, rivers, or coastal oceans in isolation. This fragmented approach has limited the identification of shared mechanisms and system-specific controls governing bloom dynamics. Moreover, most existing reviews emphasize individual ecosystems or specific phases of bloom development, leaving a comprehensive synthesis of the entire bloom life cycle across aquatic environments largely absent.

It has become evident that blooms and their associated toxins now propagate across ecosystem boundaries through the freshwater–marine continuum,[4] while climate warming is expanding bloom distributions toward higher latitudes and intensifying cryospheric algal blooms that accelerate ice and snow melt.[5,6] At the same time, emerging environmental risks, including antibiotic resistance genes and microplastic pollution, are increasingly linked to bloom processes across aquatic systems.[7,8] Although lake, river, reservoir, and marine research communities have each generated substantial system-specific knowledge, integrating these parallel advances is essential for understanding bloom dynamics in an increasingly connected and rapidly changing world. The need for a cross-system perspective is, therefore, becoming increasingly urgent.

Here, we propose that phytoplankton blooms can be viewed through a common five-stage life-cycle framework consisting of recruitment, proliferation, persistence, decline, and fate. This framework is intended as a heuristic tool for cross-system comparison rather than a rigid classification scheme. *Recruitment* describes the transition of dormant or surviving cells to active growth.[3,9] *Proliferation* involves positive net population growth and biomass accumulation.[10,11] *Persistence* represents the maintenance of elevated biomass despite ongoing losses.[12-15] *Decline* occurs when losses exceed gains,[16-19] and *fate* encompasses the post-bloom redistribution, transformation, and recycling of organic matter.[16] Across systems, these stages are mediated by eco-physiological adaptations such as flexible nutrient acquisition, oxidative stress tolerance, and inducible structural defenses, which enable phytoplankton to thrive under highly variable environmental conditions, including those of cryospheric habitats.[20-23]

Using this framework, we synthesize bloom dynamics across aquatic ecosystems, while treating cryospheric environments as a distinct comparative case study because their bloom development is governed primarily by ice

Table 1. Functional bloom-forming groups, dominant adaptive strategies, and associated bloom stages across aquatic systems.

Functional group	Representative taxa	Dominant adaptive traits	Most influenced bloom stages	Dominant aquatic systems	References
Buoyant cyanobacteria	*Microcystis*, *Dolichospermum*, *Aphanizomenon*, *Planktothrix*	Gas vesicles, nitrogen fixation, polyphosphate storage, colony formation	Recruitment, proliferation, persistence	Lakes, reservoirs, slow-flow rivers	Refs.[24-26]
Opportunistic diatoms	*Pseudo-nitzschia*, *Aulacoseira*, *Stephanodiscus*	Rapid nutrient uptake, resting stages, turbulence tolerance, chain formation	Proliferation, decline, fate	Rivers, coastal oceans, large lakes	Refs.[27-31]
Filamentous macroalgae	*Cladophora*, *Spirogyra*, *Ulothrix*,	Filamentous growth, substrate attachment, rapid nutrient uptake, desiccation tolerance	Proliferation, persistence	Rivers, streams, shallow lakes	Ref.[32]
Mixotrophic flagellates	*Alexandrium*, *Karenia*, *Prymnesium*, *Dinobryon*	Mixotrophy, vertical migration, allelopathy, cyst formation	Persistence, decline	Coastal systems, estuaries, reservoirs	Refs.[33-35]
Benthic mat-formers	*Lyngbya*, *Microcoleus*, *Didymosphenia*	Surface attachment, mucilage production, stress tolerance	Persistence, fate	Rivers, shallow lakes	Refs.[24,36]
Stress-tolerant freshwater flagellates	*Gonyostomum*, *Euglena*, *Synura*	Organic matter utilization, salinity tolerance, low-light adaptation	Persistence	Humic lakes, nutrient-rich ponds	Refs.[36,37]

and snow physics rather than the hydrological and stratification processes characteristic of liquid-water systems. By identifying both common principles and system-specific mechanisms, we provide an integrated perspective on phytoplankton bloom dynamics across the full spectrum of aquatic environments.

REVIEW METHODOLOGY

We conducted a systematic search of Web of Science, Scopus, and Google Scholar using keyword combinations including "phytoplankton bloom life cycle", "algal blooms", "cyanobacteria bloom mechanisms", "bloom recruitment", "bloom persistence", "bloom decline", "cross-system bloom comparison", "cryospheric phytoplankton", "antibiotic resistance genes bloom", "iron limitation neurotoxin", and "plastisphere carbon export". The search covered publications from 2000 to 2026, with seminal foundational studies included regardless of date, as they were necessary to establish foundational concepts or historical context. We included studies if they reported mechanisms of bloom initiation, development, decline, or fate across lakes, reservoirs, rivers, coastal or marine environments, or cryospheric systems. Review articles, experimental studies, field observations, and modeling studies were all considered.

FUNCTIONAL BLOOM-FORMING GROUPS AND DOMINANT ADAPTIVE STRATEGIES ACROSS AQUATIC SYSTEMS

Phytoplankton blooms are formed by phylogenetically diverse taxa, yet bloom success depends primarily on convergent ecological strategies rather than taxonomy alone (Table 1). Across aquatic systems, bloom-forming species exploit favorable environmental windows through nutrient acquisition, buoyancy regulation, dormancy formation, mixotrophy, and stress tolerance, which collectively structure progression through bloom stages.

Despite phylogenetic differences, major groups converge functionally. Cyanobacteria dominate eutrophic lakes and reservoirs via buoyancy regulation, nitrogen fixation, and phosphorus storage.[24-26] Diatoms dominate rivers, coastal upwelling systems, and large lakes through rapid growth rates, turbulence tolerance, and resting-stage formation,[27-31] while filamentous macroalgae such as *Cladophora*, *Spirogyra*, and *Ulothrix* also form extensive benthic and suspended mats in rivers and shallow lakes by exploiting substrate attachment and rapid nutrient uptake during low-flow, nutrient-rich conditions.[32] Mixotrophic flagellates persist under nutrient variability through flexible nutritional modes and allelopathy.[33-35] Benthic mat-forming taxa thrive in shallow and flowing environments through substrate attachment, mucilage production, and tolerance to hydrodynamic disturbance.[24,36] Stress-tolerant freshwater flagellates are often associated with humic and nutrient-rich waters, where low-light adaptation, salinity tolerance, and utilization of organic matter enhance persistence.[36,37]

Despite phylogenetic and ecological diversity across aquatic systems, bloom-forming groups share a common underlying logic: their dominant adaptive strategies collectively govern how blooms are initiated, sustained, and terminated. This convergence forms the mechanistic foundation of the unified five-stage bloom framework developed in this review, whose physiological and ecological bases are explored in the following section.

MECHANISTIC PHYSIOLOGICAL AND ECOLOGICAL STRATEGIES REGULATING BLOOM DEVELOPMENT

Bloom development depends on coordinated physiological and ecological strategies interacting with hydrodynamics, nutrient availability, light climate, and residence time (see Texts S1-S2). The same physiological capacity may confer different ecological advantages depending on the aquatic system and bloom stage in which it operates. Therefore, bloom traits should be interpreted as system-dependent mechanisms regulating life-cycle progression rather than universally advantageous characteristics.

Physiological traits determine how phytoplankton acquire resources, tolerate stress, regulate vertical positioning, and survive unfavorable conditions (Table 2). Ecological strategies determine how bloom-forming taxa interact with physical forcing, microbial communities, grazers, and hydrodynamic disturbance (Table 3). Together, these mechanisms control bloom initiation, biomass accumulation, persistence, collapse, and post-bloom carbon processing across aquatic environments.

Taken together, these physiological and ecological strategies demonstrate that bloom dynamics emerge from interactions between conserved functional traits and system-specific environmental constraints. Recurrent mechanisms–nutrient storage, dormancy formation, buoyancy regulation, vertical migration, and microbial interactions–consistently underpin bloom success across taxa. However, their relative importance differs across lakes, reservoirs, rivers, estuaries and coastal oceans due to contrasting physical and biogeochemical controls across bloom stages. This functional convergence forms the mechanistic foundation of the unified five-stage framework proposed in this review.

MECHANISMS OF PHYTOPLANKTON BLOOM FORMATION AND DECLINE IN AQUATIC SYSTEMS

Phytoplankton blooms are episodic yet recurrent bursts of primary productivity arising from interactions between environmental forcing and physiological adaptation. Their life cycle typically proceeds through five stages – recruitment, proliferation, persistence, decline, and fate (Figure 1) – each governed by interacting physical, chemical, and biological drivers. Blooms emerge when environmental conditions (light, temperature, nutrients, and hydrodynamic retention) align with organismal capabilites such as nutrient uptake, buoyancy regulation, dormancy, and microbial interactions.[58] Key quantitative thresholds governing these transitions across systems are summarized in Table 4.

Although the underlying mechanisms of bloom formation are broadly conserved, their expression varies markedly across aquatic systems. The

Table 2. Mechanistic physiological traits controlling bloom progression across aquatic systems.

Physiological trait	Mechanistic role	Most affected bloom stage	Dominant environmental control	Most influenced system	References
Rapid nutrient uptake and storage	Supports rapid biomass accumulation and growth during transient nutrient availability	Proliferation	Nutrient pulses and residence time	Rivers, reservoirs, coastal systems	Refs.[26,38-40]
Polyphosphate storage	Alleviates phosphorus limitation and sustains prolonged growth	Persistence	Internal nutrient recycling	Lakes, reservoirs	Ref.[26]
Nitrogen fixation	Supports growth under low inorganic nitrogen conditions	Proliferation, persistence	Nitrogen limitation	Lakes, coastal systems	Refs.[4,29]
Buoyancy regulation	Maintains cells within the euphotic zone under stratified conditions	Persistence	Thermal stability and mixing depth	Lakes, reservoirs	Refs.[7,41–44]
Vertical migration	Optimizes light and nutrient acquisition across depth gradients	Persistence	Stratification and nutrient gradients	Lakes, stratified reservoirs, oceans, estuaries,	Refs.[7,44]
Mixotrophy	Supports growth during nutrient or light limitation	Persistence	Organic matter availability	Coastal systems, humic lakes	Refs.[45–49]
Resting-stage formation	Enables seasonal reseeding and survival under unfavorable conditions	Recruitment	Sediment disturbance and seasonal transitions	Lakes, rivers, coastal systems	Refs.[9,20,50]
Salinity tolerance	Supports persistence across fluctuating osmotic environments	Persistence	Salinity gradients	Estuaries, brackish waters	Refs.[51–55]
Oxidative stress tolerance	Enhances survival under thermal and irradiance stress	Persistence, decline	Temperature and ROS exposure	Lakes, marine systems	Refs.[13,14,56,57]
Carbon concentrating mechanisms (CCMs)	Ensures inorganic carbon acquisition under high productivity	Proliferation, persistence	CO_2 limitation and pH	Lakes, oceans	Refs.[22,58–61]
Toxin biosynthesis	Reduces grazing pressure and alters food-web interactions	Persistence, decline	Nutrient stress and temperature	Freshwater and marine HAB systems	Refs.[21,62–66]

Table 3. Ecological structuring mechanisms regulating bloom dynamics across aquatic systems.

Ecological mechanism	Functional effect on bloom dynamics	Most influenced bloom stage	Dominance in lakes/reservoirs	Dominance in rivers	Dominance in coastal/ocean systems	References
Stratification and retention	Extends bloom duration and stabilizes surface biomass	Persistence	Strong	Weak–moderate	Strong	Refs.[67–69]
Hydrological regulation	Alters residence time, flushing, and nutrient retention	Recruitment, decline	Moderate	Strong	Moderate	Refs.[17,30,67]
Internal nutrient recycling	Sustains blooms after external nutrient depletion	Persistence	Strong	Weak	Moderate	Refs.[26,70,71]
Microbial interactions	Enhances nutrient regeneration and organic matter processing	Persistence, fate	Strong	Moderate	Strong	Refs.[16,72]
Viral lysis	Accelerates bloom collapse and DOM release	Decline, fate	Moderate	Weak	Strong	Refs.[16,73]
Grazing pressure	Controls biomass loss and community succession	Decline	Moderate	Moderate	Strong	Refs.[72–76]
Mesoscale circulation and fronts	Concentrates biomass and controls spatial patchiness	Proliferation, persistence	Weak	Weak	Strong	Refs.[70,77–79]
Sedimentation and export	Transfers bloom-derived carbon to sediments and deep waters	Fate	Strong	Moderate	Strong	Refs.[71,80–84]

principal environmental drivers influencing bloom initiation and termination are summarized in Tables S1 & S2, while core processes and system-specific differences across bloom stages are detailed in Table S3.

Recruitment stage

Recruitment marks the transition from dormant benthic stocks to active pelagic populations and is a critical control point in phytoplankton bloom dynamics (Figure 2). Seasonal blooms of cyanobacteria such as *Microcystis* often originate from overwintering populations in sediments that serve as seed sources for subsequent growth in the water column. Early tracer studies demonstrated that sediment-deposited *Microcystis* can directly seed blooms in the following year, confirming the importance of benthic overwintering in eutrophic lakes.[89] Long-term observations in Lake Taihu, China showed accumulation of benthic inocula prior to spring bloom development.[85] Overwintering vegetative cells thus function as persistent seed banks that survive unfavorable conditions and reactivate when conditions improve.[90]

In lakes, recruitment typically begins in spring as increasing temperature and light stimulate benthic cells to regain metabolic activity and migrate into the water column. Overwintered *Microcystis* can resume growth at 5°C-9°C, with recruitment accelerating above ~14°C.[86] Microbial processes at the sediment–water interface promote recruitment by modifying nutrient and oxygen conditions that facilitate germination and upward migration.[91] Similar processes occur in shallow systems such as Lake Taihu, where sediment seed banks contribute substantially to early-season biomass.[92] Reservoirs follow similar patterns, although hydrodynamics exert stronger control. In Shanzi Reservoir, recruitment of *Microcystis* and *Oscillatoria* is promoted by warming temperatures and increasing light, while physical disturbance influences community composition.[93]

In rivers, recruitment is generally constrained by high flow and limited

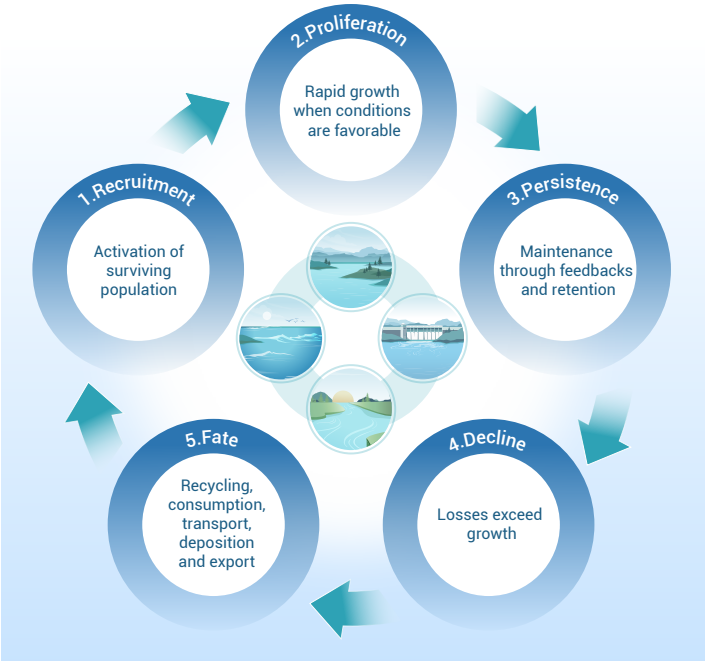

Figure 1. Unified five-stage life cycle of phytoplankton blooms across aquatic systems.

retention, though backwaters and slow-flowing reaches allow benthic propagules to establish pelagic populations. In the Xiangxi River, overwintering cyanobacteria influence phosphorus and nitrogen cycling and contribute to blooms during low-flow periods.[94] Coastal and marine systems also recruit from benthic resting stages. In the San Francisco Estuary Delta, California USA, overwintering *Microcystis* contributes to summer blooms, while resting stages of diverse phytoplankton taxa in shallow coastal sediments respond to seasonal increases in temperature and light, influencing bloom timing.[95,96]

Although recruitment across aquatic systems relies on benthic seed banks, dominant controls differ among environments. Lakes are regulated primarily by temperature and light, reservoirs by thermal conditions and hydrodynamics, rivers by hydrological windows that permit cell retention, and estuarine and coastal systems by seasonal mixing and environmental transitions. Experimental desiccation–germination studies demonstrated successful recruitment of cyanobacteria, diatoms, green algae, and phytoflagellates from dormant sediment stages, confirming the importance of resting propagules as biological reservoirs linking benthic and pelagic phases.[97] Recruitment success declined significantly at 34°C, highlighting the sensitivity of sediment seed banks to climatic warming.[97]

A key mechanistic distinction lies in the recruitment trigger. In stratified lakes, recruitment is primarily temperature-driven,[86,91] whereas in reservoirs water-level fluctuations and hydrodynamic drawdown resuspend benthic propagules and alter recruitment timing independently of temperature.[17] In rivers, recruitment depends on reduced flow and shear stress, allowing cell retention.[94] These differences require temperature-based triggers in lake models and flow-regime variables in river and reservoir models for accurate bloom forecasting.[9,17,94]

Theoretical synthesis. Across aquatic systems, recruitment conforms to the law of threshold activation, whereby dormant propagules transition to active growth only after system-specific environmental thresholds are exceeded. Although the dominant trigger differs among systems – thermal activation in lakes, hydrodynamic relaxation in rivers and reservoirs, and advective–mixing transitions in coastal environments – the underlying principle remains the same. Recruitment is therefore best viewed as a threshold-dependent phase transition linking benthic seed banks to pelagic bloom formation rather than a continuous response to environmental forcing.

Proliferation stage

Once cells enter the water column, the proliferation stage begins, characterized by rapid biomass accumulation of one or a few dominant phytoplankton species. Under favorable conditions, populations can form visible surface blooms (Figure 3). Elevated temperature, high nutrient availability, and stable hydrological conditions promote this growth phase.[98,99] Following recruitment, cyanobacteria such as *Microcystis*, *Dolichospermum*, and *Aphanizomenon* rapidly regain metabolic activity and often enter exponential growth within days.[9,100,101]

Although proliferation occurs when growth exceeds physical losses, its dominant controls vary among aquatic systems. In lakes, nutrient availability, particularly nitrogen and phosphorus, primarily regulates biomass accumulation, while external loading and internal recycling sustain growth under eutrophic conditions.[34,102] Cyanobacteria gain a competitive advantage through atmospheric nitrogen fixation, luxury phosphorus uptake,[26,40] and enhanced metabolism at temperatures above ~25°C,[34,102] as demonstrated in Lake Taihu.[103]

Reservoirs exhibit similar nutrient–temperature controls but are additionally influenced by hydrodynamics. Thermal stratification maintains buoyant taxa within the euphotic zone, while nutrient retention from inflowing rivers concentrates resources for bloom expansion. Observations from Dawangtan Reservoir demonstrate a strong relationship between elevated nitrogen and phosphorus concentrations and recurring cyanobacterial blooms.[104]

In rivers, proliferation is constrained primarily by flow and residence time. High discharge and turbulence export cells downstream, whereas slower-flowing reaches, backwaters, and impounded sections create retention zones that support rapid growth. In the Yangtze River Basin, prolonged warming increased phytoplankton abundance and cyanobacterial dominance, highlighting the importance of thermal forcing even in dynamic environments.[105]

In estuarine and coastal marine systems, proliferation depends on physical forcing and episodic nutrient delivery. River discharge, upwelling, and lateral transport supply nutrients that stimulate rapid growth. In the East China Sea, enhanced riverine input and subsurface upwelling intensified phytoplankton proliferation during post–El Niño summers,[106] while interactions among freshwater inflows, tides, and wind-driven mixing create favorable but often transient bloom conditions.[107]

A key mechanistic distinction among systems is the limiting resource. In eutrophic lakes and reservoirs, phosphorus and nitrogen availability and temperature jointly regulate bloom expansion, with cyanobacteria benefiting from efficient phosphorus recycling and nitrogen fixation.[29,102] In rivers, physical retention determines whether growth exceeds flushing losses. In marine and coastal environments, micronutrients, particularly iron availability, can also regulate neurotoxin production in *Pseudo-nitzschia*.[4,79]

Recent evidence has revealed a direct mechanistic connection between iron stress and β-N-methylamino-L-alanine (BMAA) production in marine diatoms.[4] Under iron-limited conditions, transcriptomic analyses identified cysteine synthase (CysK) as a key enzyme involved in BMAA biosynthesis. CRISPR/Cas9-mediated knockout of CysK completely abolished BMAA production, while restoration of the enzyme fully recovered toxin synthesis, providing the first direct functional evidence for a CysK-dependent BMAA biosynthetic pathway.[4] The proposed pathway involves endogenous methylamine and cysteine-containing peptides that are catalytically converted into BMAA, with BMAA-containing proteins subsequently localized within the endoplasmic reticulum and Golgi apparatus.[4]

The regulatory context of BMAA production extends beyond diatoms. In cyanobacteria, current evidence suggests that BMAA may be synthesized through 3-N methylation of 2,3-diaminopropanoic acid (2,3-DAP), with S-adenosyl-methionine serving as the methyl donor, although the complete pathway remains unresolved.[108] This taxonomic diversity suggests that nutrient- and iron-stress-induced BMAA production may be more widespread among phytoplankton than currently recognized.

Beyond toxin synthesis, BMAA has broad metabolic consequences. Proteomic studies demonstrate that BMAA disrupts tightly coupled nitrogen and carbon metabolic pathways in cyanobacteria, inhibiting nitrogen fixation and heterocyst differentiation under nitrogen-starved conditions.[109] Additional studies show that BMAA alters amino acid and purine synthesis, disrupts DNA transcription and protein translation, impairs CO_2 fixation and photosystem function, and induces oxidative stress, chaperone responses, and SOS-repair pathways.[109] Consequently, BMAA acts not only as a toxin but also as a mediator of widespread cellular stress responses triggered by nutrient

Table 4. Quantitative environmental thresholds regulating bloom life-cycle transitions across aquatic systems.

Life-cycle stage	Environmental driver	Quantitative threshold value	Mechanistic implication	References
Recruitment	Water temperature (*Microcystis* activation)	15°C–20°C[a]	Initiates reactivation of overwintering benthic inocula and promotes upward recruitment into the water column	Ref. [85]
	Temperature threshold for cyanobacterial dominance	> 25°C[b]	Favors cyanobacteria due to superior thermal growth optima relative to eukaryotic phytoplankton	Ref.[11]
	Sediment inoculum depth persistence	Detected to 8–10 m depth[c]	Overwintering pelagic *Microcystis* populations remain viable across depth gradients, enabling seasonal reseeding	Ref.[86]
	Light availability for diatom rejuvenation	> 20–40 μmol photons m^{-2} s^{-1}[d]	Triggers resting-cell activation and photosynthetic re-entry	Ref.[31]
Proliferation	Total phosphorus	10–60 μg L^{-1} TP[e]	Supports cyanobacterial dominance depending on taxa-specific nutrient thresholds	Ref.[18]
	DIN:TP ratio	< 10–15[f]	Nitrogen limitation favors diazotrophic cyanobacteria and bloom intensification	Ref.[18]
	Thermal optimum	25°C–32°C[g]	Maximizes cyanobacterial growth and toxin production	Ref.[21]
	Dissolved iron limitation	< 1–2 nM Fe[h]	Activates cysteine synthase-linked domoic acid biosynthesis in marine diatoms	Ref.[4]
Persistence	Surface temperature	25–30°C sustained[i]	Maintains buoyancy regulation and suppresses competing taxa	Ref.[25]
	Hydraulic residence time	> 3–10 days[j]	Enables biomass accumulation and prevents advective washout	Ref.[19]
	Water-column stability	Stratification > 2–4 weeks[k]	Promotes vertical segregation and persistent surface scum formation	Ref.[25]
Decline	Reservoir flushing	Residence-time reduction > 40%–60%[l]	Destabilizes blooms through hydraulic displacement	Ref.[30]
	Destratification / mixing depth exceedance	Mixing depth > euphotic depth[m]	Causes light limitation and physiological collapse	Ref.[42]
	Salinity stress	> 5–8 PSU (freshwater cyanobacteria) [n]	Disrupts osmotic regulation and colony stability	Ref.[52]
Fate	Hypoxia threshold	DO < 2 mg L^{-1}[o]	Drives fish mortality, nutrient regeneration, and benthic impairment	Ref.[87]
	Internal phosphorus recycling during collapse	Sediment P release increases when DO < 2–3 mg L^{-1} [p]	Re-seeds subsequent bloom cycles	Ref.[71]
	Carbon export attenuation	20%–60% flux attenuation in upper mesopelagic[q]	Determines bloom-derived carbon sequestration efficiency	Ref.[88]

Notes: [a] Reported for overwintering and recruitment of *Microcystis* in temperate freshwater systems; this is not a universal recruitment threshold for all cyanobacteria. [b] Represents a warm-water condition favoring cyanobacterial dominance; the response varies among taxa, climate zones, nutrient conditions, and mixing regimes. [c] Refers to reported sediment inoculum depths for overwintering *Microcystis*; depth varies among systems and should not be generalized to all cyanobacteria. [d] Reported for rejuvenation of diatom resting cells; light requirements vary among taxa, resting stages, and environmental conditions. [e] Represents a broad eutrophic range associated with cyanobacterial dominance; this is not a universal phosphorus threshold for bloom formation. [f] An empirical nutrient-ratio range associated with conditions favoring diazotrophic cyanobacteria; applicability depends on nutrient availability and taxonomic composition. [g] Reported as a favorable temperature range for growth and/or toxin production in studied freshwater cyanobacteria; thermal optima vary among taxa and strains. [h] Applies primarily to iron-limited marine diatoms in the cited study and should not be extrapolated to freshwater phytoplankton or non-diatom taxa. [i] Represents sustained warm-water conditions associated with cyanobacterial bloom persistence; the threshold varies with taxa, nutrient status, light, and hydrodynamics. [j] Indicates a residence-time range that may permit phytoplankton biomass accumulation; the effective threshold is highly system-specific and depends on system size and growth rate. [k] Represents prolonged stratification favorable for bloom persistence in stratified lakes and reservoirs; the required duration varies with hydrodynamics and taxa. [l] Represents a substantial flushing condition reported for bloom management; effectiveness is system- and operation-dependent. [m] Indicates reduced average light exposure of phytoplankton; the effect depends on mixing dynamics, light climate, and taxon-specific photoacclimation. [n] Represents salinity conditions associated with stress in freshwater cyanobacterial communities; tolerance varies among taxa and strains. [o] Operationally indicates severe hypoxia; biological responses vary with taxon, temperature, exposure duration, and habitat. [p] Represents oxygen-deficient conditions that may enhance sediment phosphorus release; the response is sediment- and system-dependent. [q] Represents reported attenuation of sinking carbon flux in the upper mesopelagic ocean; it is not directly applicable to freshwater systems and varies among oceanic environments.

limitation.

The ecological implications of this mechanism operate across multiple scales. At the cellular scale, in iron-limited marine and coastal systems, BMAA production is activated when iron limitation restricts further biomass accumulation, linking toxin synthesis directly to physiological stress.[4] At the ecosystem scale, the prevalence of iron-limited diatoms in many marine environments suggests that BMAA production may represent a widespread but underappreciated component of bloom ecology.[4] At the public health

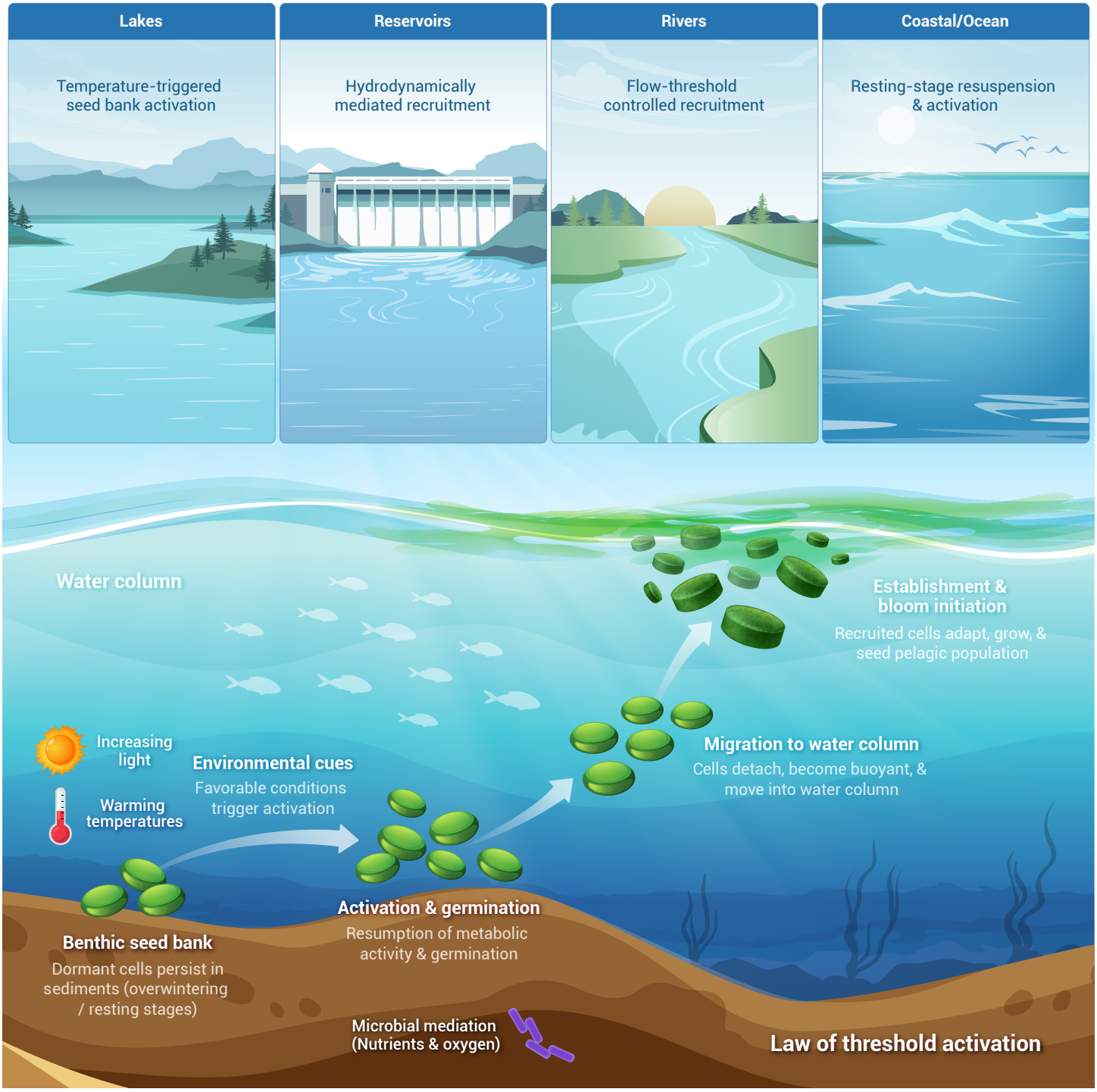

Figure 2. Recruitment stage across aquatic systems Dormant propagule transition to active pelagic populations through temperature-triggered seed bank activation in lakes, hydrodynamically mediated recruitment in reservoirs, flow-threshold controlled recruitment in rivers, and resting-stage resuspension and activation in coastal and marine systems.

scale, BMAA is a neurotoxic non-protein amino acid associated with neurodegenerative disease and may enter higher trophic levels through marine food webs, creating an additional risk pathway associated with bloom proliferation.[4]

Theoretical synthesis. Proliferation follows the law of resource-retention optimization, whereby bloom expansion occurs when resource acquisition rates exceed physical loss rates. Although the limiting resource differs among systems, including phosphorus and nitrogen availability, in eutrophic freshwaters, physical retention in rivers, iron in offshore marine systems, and light in low-transparency environments—successful bloom development universally depends on maximizing access to the scarcest growth-limiting resource within a favorable hydrodynamic window.

Persistence stage

Following rapid proliferation, the persistence stage is characterized by the maintenance of high phytoplankton biomass for weeks to months under favorable environmental, nutrient, and hydrological conditions (Figure 4). During this phase, bloom-forming taxa balance growth against losses from grazing, sedimentation, and microbial degradation, maintaining a dynamic equilibrium between physiological resilience and ecological pressures.[25,102] In shallow eutrophic lakes such as Lake Rotorua, New Zealand, buoyant *Micro-*

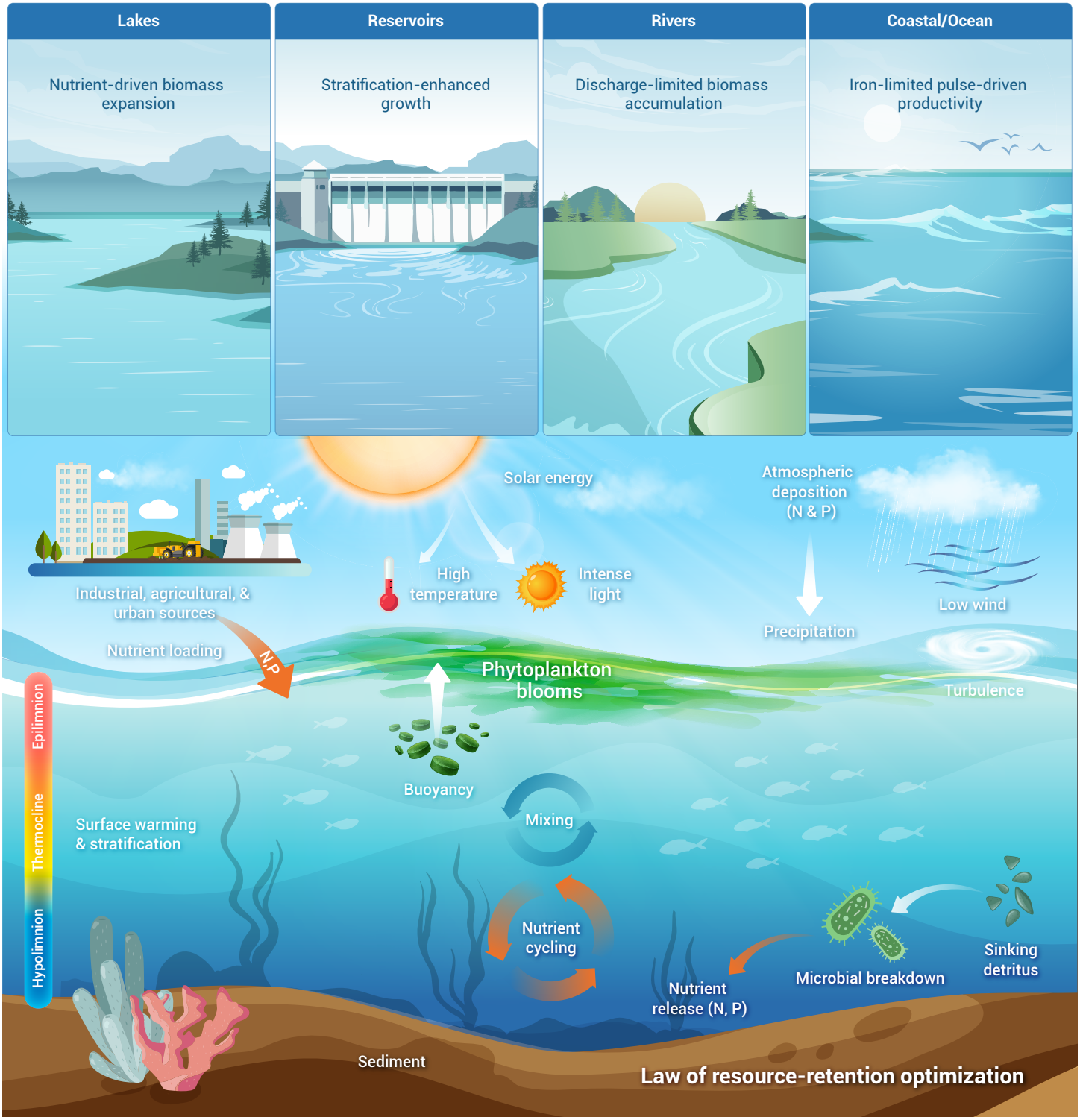

Figure 3. Proliferation stage across aquatic systems Resource acquisition exceeds loss rates through nutrient-driven biomass expansion in lakes, stratification-enhanced growth in reservoirs, discharge-limited biomass accumulation in rivers, and iron-limited pulse-driven productivity in coastal and marine systems.

cystis dominate surface waters under warm conditions supported by a favorable light environment and internal nutrient cycling.[10]

A central mechanism underlying persistence is efficient resource acquisition coupled with nutrient regeneration. Cyanobacteria store excess phosphorus as intracellular polyphosphate (polyP), enabling growth during low external nutrient supply, while utilizing multiple nitrogen sources, including ammonium, nitrate, and atmospheric N_2 through heterocyst-mediated fixation.[20,26] Internal phosphorus recycling can satisfy much of the nutrient requirements during prolonged blooms. These advantages are reinforced by phycosphere-associated microbial communities that enhance nutrient regeneration and stabilize biomass.[72] Cyanotoxin production may further promote persistence by reducing grazing pressure and weakening top-down control.[62]

Although these mechanisms occur across aquatic systems, their relative importance differs. In lakes, persistence is sustained by thermal stratification, buoyancy regulation, and internal nutrient cycling. Reservoirs share these controls but are additionally influenced by hydrological regulation, with sustained *Microcystis* blooms associated with favorable nutrient ratios, thermal stability, nutrient-rich inflows, and reduced vertical mixing.[110]

In rivers, persistence is generally limited by flow, but warm temperatures and reduced discharge can support extended bloom dominance. In the

Moselle River, Western Europe, low-flow conditions promoted persistent *Microcystis* blooms.[45] Microcystin concentrations during this stage reflect the balance among production, degradation, and ecological feedbacks rather than biomass alone.[111]

Coastal and marine systems similarly depend on physical stability and nutrient availability. In the Baltic Sea, nitrogen-fixing cyanobacteria maintain extensive summer blooms under stratified, low-flushing conditions, reinforced by episodic upwelling and riverine inputs.[112] Overall, nutrient recycling, physical stability, and biotic interactions universally sustain persistence, although their relative roles differ among aquatic systems.

Recent evidence suggests that climate change may strengthen bloom persistence by enhancing the physiological resilience of bloom-forming taxa. Repeated climatic extremes increase resistance to environmental stressors, promoting prolonged dominance and bloom recurrence.[113]

An emerging and increasingly important dimension of bloom persistence is the development of antibiotic resistance gene (ARG) "hotspots" within bloom-associated microbial communities under warming conditions. Experimental warming from 22°C to 24°C caused substantial microbial community restructuring, with cyanobacterial abundance increasing from 6.11% to 20.53%. Toxin-producing families including *Microcystaceae,* and *Nostocaceae* increased significantly, while the microcystin synthesis gene *mcy* exhibited a strong positive relationship (R^2 = 0.88) with cyanobacterial abundance.[7] Concurrently, ARG abundance increased markedly, with multidrug resistance genes accounting for approximately 50.82% of total ARGs across warming treatments.[7]

The mechanistic pathway linking warming to ARG enrichment appears to involve reactive oxygen species (ROS) as a central regulatory trigger. Temperature perturbations enhance bacterial conjugative transfer by promoting ROS generation and cellular aggregation, while simultaneously stimulating antioxidant defenses, SOS responses, and the energetic processes required for horizontal gene transfer.[114] Experimental addition of ROS reproduced the effects of warming on cyanobacterial proliferation,[7] confirming oxidative stress as a mechanistic link connecting elevated temperature, bloom formation, and ARG enrichment.[115]

Field observations further demonstrate the scale of ARG proliferation during bloom persistence. In Lake Taihu, 122 ARGs and nine mobile genetic elements were detected across bloom phases.[116] These genes represented eight resistance categories, including aminoglycoside, β-lactam, multidrug, fluoroquinolone, and tetracycline resistance, and encompassed four major resistance mechanisms: antibiotic deactivation (44.2%), efflux pumps (40.7%), cellular protection (10.6%), and unknown mechanisms (4.5%).[116] ARG abundance increased during active bloom phases, while cyanobacteria, particularly *Microcystis*, served as important reservoirs and dissemination platforms through mobile genetic elements. Furthermore, ARG-hosting bacteria attached to cyanobacterial aggregates persisted longer than free-living bacterial populations, increasing the likelihood of environmental transmission.[116]

The ecological implications of ARG enrichment operate across multiple scales. At the ecosystem level, cyanobacterial blooms act as important drivers of ARG accumulation and dissemination, with climate warming and eutrophication simultaneously increasing bloom frequency, intensity, and duration worldwide.[7] At the public health level, bloom-affected waters used for drinking water, irrigation, aquaculture, and recreation can simultaneously concentrate cyanotoxins and ARG-carrying microorganisms, creating a convergent One Health risk that cannot be effectively addressed by managing eutrophication or antimicrobial resistance independently.[7]

Theoretical synthesis. Persistence conforms to the law of feedback stabilization, whereby blooms actively reinforce the physicochemical conditions that sustain them through nutrient recycling, microbiome-mediated resource regeneration, buoyancy regulation, toxin-mediated grazer suppression, and stress-adaptive metabolic plasticity. These positive feedback mechanisms explain why bloom duration frequently exceeds predictions based solely on external nutrient supply and why persistent blooms often become increasingly resistant to environmental perturbations over time.

Decline Stage

Bloom stability is never absolute. The decline stage marks the reduction of phytoplankton biomass after persistence, driven by environmental stress, nutrient limitation, biotic interactions, and physical perturbations (Figure 5). Bottom-up controls intensify as limiting nutrients such as phosphorus, nitrogen, or silicate become depleted, while dense surface accumulations increase self-shading, reducing light availability and suppressing primary production. As decline progresses, communities often shift from large bloom-forming taxa toward smaller opportunistic phytoplankton and heterotrophic organisms.[2,117,118]

Top-down processes further accelerate bloom collapse. Micro- and mesozooplankton grazing can rapidly remove biomass, while phenotypic plasticity, such as inducible bristle formation, may temporarily modify grazing vulnerability.[15] Viral infections represent another major mortality pathway, converting particulate organic matter into dissolved organic matter through cell lysis.[16] Abiotic stressors, including hydraulic flushing, excessive irradiance, ultraviolet exposure, and turbulent mixing, further contribute to biomass loss.[13]

In lakes, decline is commonly associated with nutrient exhaustion and physiological stress. Bioavailable phosphorus and nitrogen can become depleted during prolonged blooms,[71] while high irradiance and temperature fluctuations impair metabolism and photosynthetic performance, with Fv/Fm declining by approximately 30%–50% during bloom senescence.[12,57] At the cellular level, a specific mortality mechanism has recently been resolved in *Microcystis*: intracellular labile iron overload catalyzes lipid peroxidation, triggering ferroptotic cell death. Oxidized lipid products released from dying cells can destabilize neighboring cells, propagating lipid peroxidation and producing the nonrandom, spatially clustered mortality observed within natural colonies.[119] This bystander-amplification mechanism provides a cellular basis for rapid, coordinated bloom collapse once physiological stress exceeds cellular buffering capacity.[119] Biomass loss is further enhanced by colony sedimentation, as gas vesicle collapse and aggregation of extracellular polymeric substances increase sinking rates, transferring cells to sediments where they either decompose or contribute to future recruitment.[47,100]

Reservoir decline reflects nutrient reduction and hydrodynamic regulation. Water-level fluctuations, flushing, and reservoir operations reduce nutrient concentrations, increase shear stress, and disrupt favorable bloom conditions. In the Three Gorges Reservoir, hydrological management reduced cyanobacterial biomass by approximately 67%–75%, accompanied by nearly 20% declines in total nitrogen and phosphorus.[17]

In rivers, hydrodynamic forcing dominates decline. Short residence times and advective transport export phytoplankton faster than growth can replenish them, while high-discharge events and managed flushing dilute nutrients, disrupt vertical positioning, and increase grazing pressure.[32] Controlled flushing in the lower-middle reaches of the Hanjiang River successfully terminated both diatom and cyanobacterial blooms.[30]

Coastal and marine systems decline through nutrient limitation, grazing, viral lysis, and physical disturbance. In the Southern Ocean, viral lysis accounts for approximately 58% of seasonal phytoplankton carbon loss, redirecting carbon into microbial recycling pathways.[73] Wind-driven mixing, storms, tidal flushing, and upwelling further destabilize blooms by altering nutrient distributions, reducing light availability, and dispersing phytoplankton populations.[120]

Although the dominant drivers vary among systems, bloom collapse universally reflects the interaction of resource limitation, biological losses, and physical disturbance. A notable cross-system pattern emerges along a residence-time gradient. Long-residence systems such as the Southern Ocean allow virus–host interactions to develop sufficiently for viral lysis to become a dominant loss pathway,[73] whereas rivers with short residence times are primarily controlled by physical export. Reservoirs occupy an intermediate position, where hydrological management can shift decline from biologically driven losses toward physically driven removal, as demonstrated in the Three Gorges Reservoir.[17] Climate-driven hydrological changes may therefore systematically alter bloom decline, with consequences for carbon cycling, toxin dynamics, and downstream biomass transport.

Theoretical synthesis. Decline conforms to the law of disturbance-driven reset, whereby bloom collapse occurs when external forcing exceeds the stabilizing capacity of bloom-maintaining feedbacks. Although the dominant

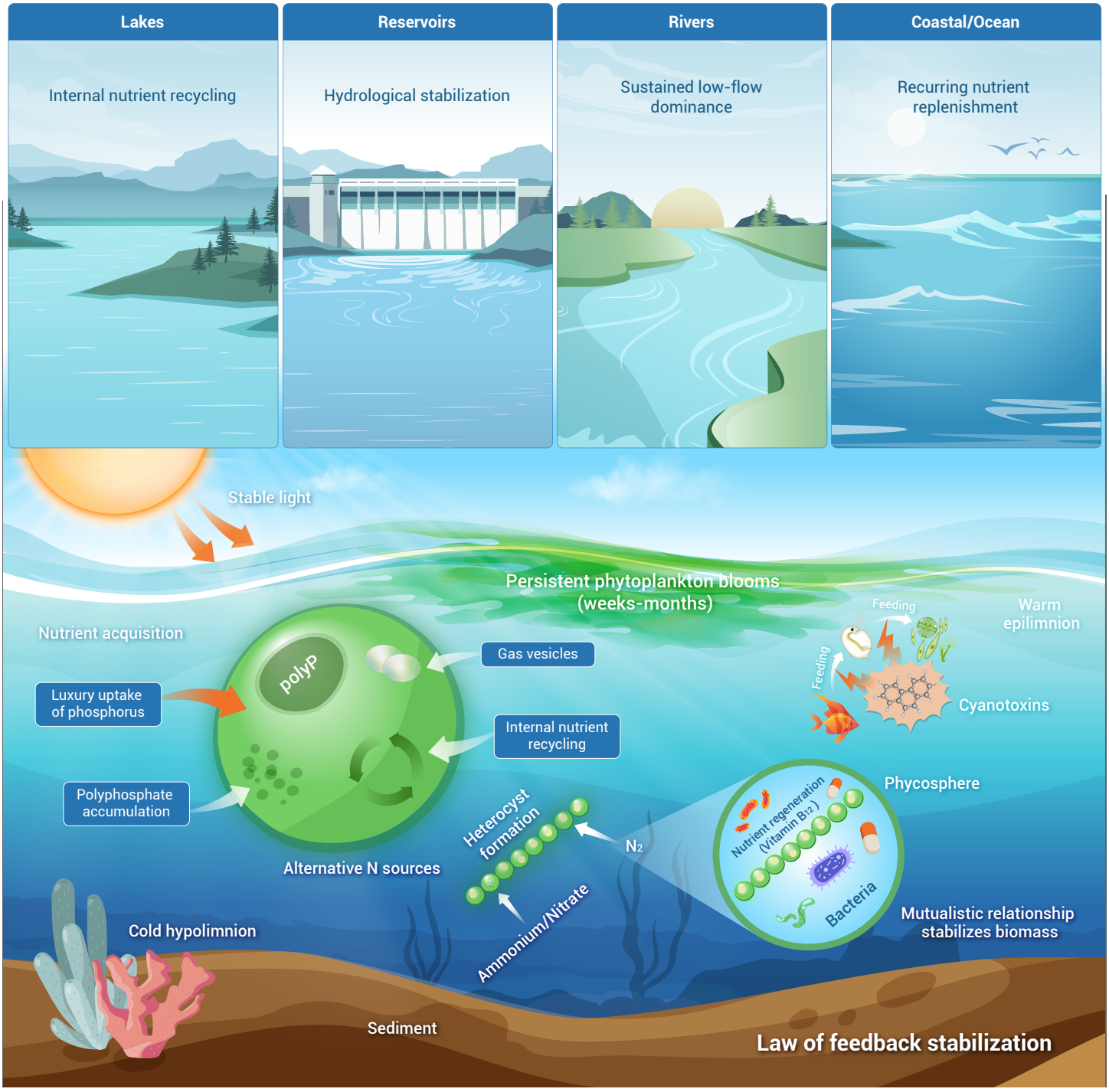

Figure 4. Persistence stage across aquatic systems Positive feedback sustains biomass through internal nutrient recycling in lakes, hydrological stabilization in reservoirs, sustained low-flow dominance in rivers, and recurring nutrient replenishment in coastal and marine systems.

reset mechanism varies among systems, including nutrient exhaustion, flushing, turbulent disruption, grazing pressure, and viral lysis, all function as threshold disturbances that terminate bloom persistence and initiate ecosystem reorganization.

Bloom fate

After a phytoplankton bloom collapses, the accumulated biomass is redistributed, transformed, and recycled through a combination of biological, chemical, and physical processes that determine its ecological fate (Figure 6). A substantial fraction enters aquatic food webs through grazing by zooplankton and other consumers, which convert phytoplankton biomass into secondary production and fecal pellets. These pellets may be recycled within surface waters or exported downward, particularly in stratified lakes and marine systems.[121] In many oceanic environments, grazing represents the dominant biomass-removal pathway; polar observations suggest that herbivory accounts for approximately 90% of bloom losses, while particle export contributes significantly to deep-ocean carbon sequestration.[121]

Microbial decomposition and particle aggregation provide additional controls on bloom fate. Microbial remineralization, viral lysis, and zooplankton-mediated fragmentation regulate whether organic carbon remains within surface waters or is exported to deeper layers.[16,88] Microplastic-associated "plastisphere" biofilms further modify these processes. Plastic–algal aggregates can either accelerate sinking when sufficiently dense or retain biomass near the surface when buoyant, altering natural carbon fluxes.[122] Plastisphere microbiomes may also modify decomposition pathways, affecting the balance between CO_2 production and dissolved organic carbon formation

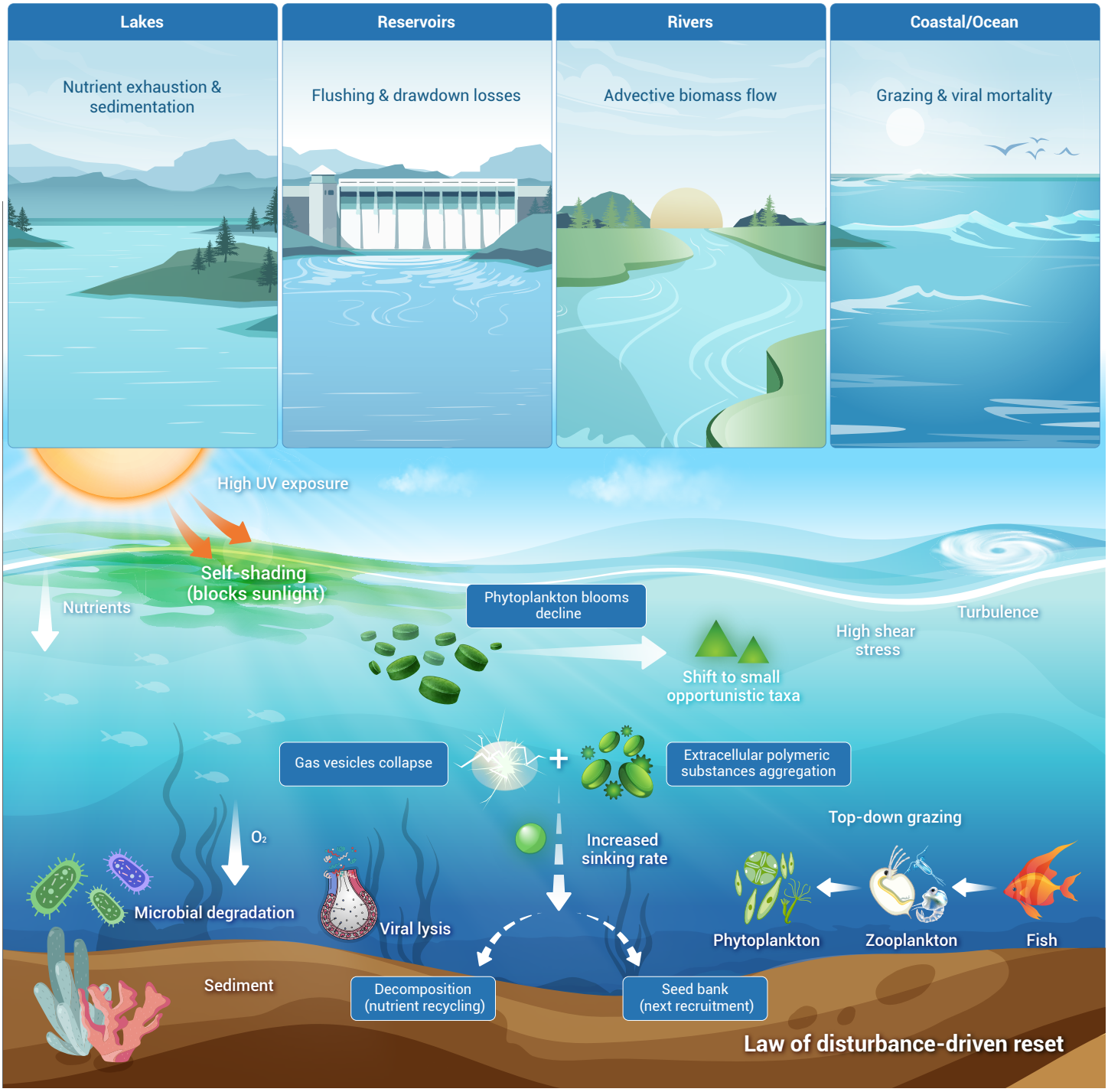

Figure 5. Decline stage across aquatic systems Loss processes exceed growth through nutrient exhaustion and sedimentation in lakes, flushing and drawdown losses in reservoirs, advective biomass export in rivers, and grazing and viral mortality in coastal and marine systems; the dominant loss mechanism is governed by water residence time across all system types.

during bloom decay.

In shallow lakes and reservoirs, bloom biomass is largely retained locally. Cyanobacterial detritus forms sediment mineralization hotspots, while microbial degradation, co-metabolism, partial sedimentation, and CO_2 release dominate bloom fate.[123] Rivers exhibit a contrasting pattern, as rapid flow and turbulence prevent substantial biomass accumulation. Dead phytoplankton and detrital material are transported downstream, where they are diluted, consumed, mineralized, or incorporated into downstream lakes, reservoirs, and estuaries, thereby contributing to longitudinal carbon transport.[124]

Marine systems exhibit a stronger coupling between bloom fate and the biological carbon pump. Aggregated phytoplankton and fecal pellets sink from the euphotic zone, transferring organic carbon to deeper waters, as documented in subarctic iron-stimulated blooms.[125] Modeling studies indicate that this export is a major driver of seasonal carbon sequestration and nutrient redistribution.[126] Bloom collapse also supplies dissolved organic carbon that supports microbial metabolism and long-term carbon storage.[127]

Overall, bloom fate varies according to hydrodynamics, sediment interactions, and trophic pathways. Lakes and reservoirs primarily retain biomass, rivers export it longitudinally, and oceans combine surface recycling with substantial vertical export. Although microbial decomposition and trophic transfer are universal processes, their relative importance varies with residence time and ecosystem structure.

Microplastics can act as novel ecological substrates, influencing bloom-associated microbial communities (see the plastisphere section for details).

Plastic debris provides a persistent substrate for microbial colonization and supports biofilm development across diverse aquatic environments.[8] Because this artificial habitat can facilitate microbial dispersal and alter ecosystem functioning, its biogeochemical significance has attracted growing attention.

Current evidence indicates that the plastisphere modifies bloom carbon fate through three principal mechanisms. First, plastisphere microbial communities differ substantially from surrounding planktonic communities and natural particle-associated assemblages. Marine polyethylene plastispheres are often dominated by *Marinobacter*, whereas freshwater polyethylene plastispheres commonly favor *Sphingomonas*. These communities contribute to methane production in anaerobic environments and contain specialized degraders capable of metabolizing organic pollutants through enzymes such as oxygenases and hydrolases.[122] As a result, bloom-derived organic matter may be processed through different enzymatic pathways than those operating on natural particles, altering both decomposition rates and degradation products.[128]

Second, plastisphere-associated viral communities can directly influence methane cycling. Recent studies demonstrate that plastisphere viruses harbor auxiliary metabolic genes capable of modifying host methane metabolism. In addition, glycoside hydrolase genes involved in carbohydrate degradation are significantly enriched within plastisphere-associated prokaryotic communities, while genes associated with anaerobic methane oxidation occur at higher abundances than in surrounding waters.[129] Consequently, bloom-derived biomass colonized by plastisphere communities may be preferentially routed toward methane production rather than conventional CO_2 mineralization or carbon export, fundamentally altering carbon-processing pathways.

Third, quantitative evidence increasingly links microplastic-associated microbial activity with greenhouse-gas amplification. Experimental syntheses indicate that microplastic exposure increases soil CO_2 emissions by 54.3% (95% CI: 47.2%–61.5%) and CH_4 emissions by 9.7% (95% CI: 1.0%–18.5%), accompanied by increases in microorganisms involved in carbon degradation pathways.[130] Biodegradable plastics may stimulate even larger greenhouse-gas emissions than conventional plastics.[130]

The ecological implications of plastisphere-mediated carbon alteration operate across multiple scales. At the ecosystem level, eutrophication-driven bloom formation and plastic pollution become coupled processes: blooms provide abundant organic carbon, while microplastics provide microbial habitats capable of redirecting carbon toward enhanced greenhouse-gas production rather than sequestration or conventional export. At the global scale, increasing bloom frequency and rising microplastic concentrations across aquatic ecosystems suggest that this interaction may represent a growing but poorly quantified component of aquatic greenhouse-gas budgets that is not currently incorporated into most bloom life-cycle models. [8,122]

Theoretical synthesis. Fate conforms to the law of ecological legacy propagation, whereby bloom biomass continues to influence ecosystem structure and biogeochemical functioning long after visible collapse. Through sediment recruitment banks, toxin persistence, carbon export, plastisphere-mediated remineralization, and nutrient regeneration, bloom residues shape the probability, magnitude, and ecological consequences of future bloom cycles.

CRYOSPHERIC ENVIRONMENTS AS A COMPARATIVE CASE STUDY: BLOOM LIFE CYCLES GOVERNED BY ICE PHYSICS

Cryospheric phytoplankton and algal bloom systems represent an ecologically distinct boundary condition of bloom dynamics, operating under extreme constraints of temperature, irradiance limitation, seasonal freeze–thaw oscillations, and tightly coupled ice–brine physicochemical gradients. Unlike other aquatic bloom systems, cryospheric blooms are not governed by classical eutrophication or prolonged thermal stratification. Instead, their development is regulated by transient windows of ice permeability, meltwater nutrient release, brine channel connectivity, and rapid physiological acclimation to extreme photothermal variability.

Because of these unique controls, cryospheric bloom processes are treated as a separate case study rather than as part of the generalized five-stage framework. Although analogous transitions occur across all five stages, the mechanistic regulators differ fundamentally from those governing other aquatic systems. Presenting cryospheric blooms as a case study therefore allows direct comparison with the generalized framework while preserving the system-specific processes that control bloom dynamics under ice-covered conditions.

Recruitment in cryospheric systems parallels benthic seed-bank activation in lakes and coastal systems but is governed by ice physics rather than water temperature alone. In lakes, temperatures above 5°C–9°C reactivate overwintering *Microcystis* from sediments,[86] whereas in rivers reduced shear stress creates recruitment windows.[94] In cryospheric environments, the analogous trigger is the freeze–thaw transition: seasonal ice thinning, melt-pond formation, and lead opening release ice-entrained communities, such as *Nitzschia frigida* and *Melosira arctica*, into the water column.[131,132] Unlike liquid-water systems, cryospheric propagules are retained within the ice matrix, making the ice column the primary inoculum reservoir.

Recent in situ Arctic studies demonstrate that recruitment intensifies when seasonal sea-ice thickness declines below ~1 m and snow cover decreases below ~0.2–0.3 m, allowing sufficient light penetration to reactivate ice-associated phototrophs and establish under-ice chlorophyll maxima.[5] Ship-based and autonomous observations further show that bloom initiation coincides with irradiance transmission exceedingly approximately 10–20 μmol photons m^{-2} s^{-1}, representing a recruitment threshold unique to cryospheric systems.[5] Pan-Arctic analyses spanning 17 years additionally reveal that reduced sea-ice cover and enhanced overwinter phytoplankton persistence are associated with earlier bloom initiation and greater bloom intensity, while winter water-column stability influences overwinter chlorophyll concentrations and subsequent recruitment success.[133]

Proliferation is governed by a light–nutrient coupling analogous to thermal stratification in lakes but physically generated by the ice cover itself. Meltwater stratification, produced by brine rejection and glacial inflows, performs the same nutrient-retaining role as a thermocline in temperate lakes.[131,132] However, the principal limiting factor shifts from phosphorus and nitrogen in lakes and reservoirs[34,104] or iron in offshore marine systems to light availability.[107] Bloom development is therefore restricted to the narrow seasonal window during which sufficient photosynthetically active radiation penetrates the ice.

Cryospheric taxa compensate for extreme oligotrophy through exceptionally high C: N: P ratios (~509:26:1 in Greenland glacier algae), polyphosphate storage, and highly efficient nitrogen assimilation strategies.[134-136] Photoacclimation studies further demonstrate dynamic reorganization of chlorophyll and pigment stoichiometry under fluctuating irradiance, allowing positive carbon fixation under near-freezing conditions despite severe light limitation.[12] In situ Arctic observations show that mixed-layer shoaling to < 20–30 m increases photon exposure time and promotes short-lived but intense under-ice bloom events.[5] Recent observations further indicate that changes in sea-ice retreat timing and upper-ocean stratification alter bloom phenology and primary production, influencing both bloom magnitude and trophic synchronization across Arctic food webs.[137]

Persistence in cryospheric systems is shorter than in stratified lakes or Baltic cyanobacterial blooms, as bloom maintenance is constrained by melt-season duration rather than by prolonged prolonged nutrient recycling or stable stratification. In lakes, persistence is reinforced by internal phosphorus recycling and bloom-associated microbiomes,[72] while coastal systems may receive recurring nutrient inputs through upwelling.[112] In contrast, cryospheric blooms rely on transient meltwater stratification and finite nutrient pulses released from brine channels and the ice matrix.[131]

Satellite observations indicate that climate warming is extending melt seasons and expanding persistence windows, although bloom durations remain considerably shorter than those observed in temperate eutrophic systems.[6] Long-term Ross Sea observations (1998–2021) show that earlier sea-ice retreat and delayed autumn refreezing are progressively lengthening bloom persistence through ice phenology and upper-ocean stratification.[23] A synthesis of 14,800 pigment samples (1997–2023) reveals a shift from diatom-dominated communities toward cryptophyte dominance after 2016.[138] These in situ observations demonstrate that persistence is increasingly regulated by climate-driven ice dynamics rather than the nutrient-retention mechanisms that dominate temperate aquatic systems.[23] Nevertheless,

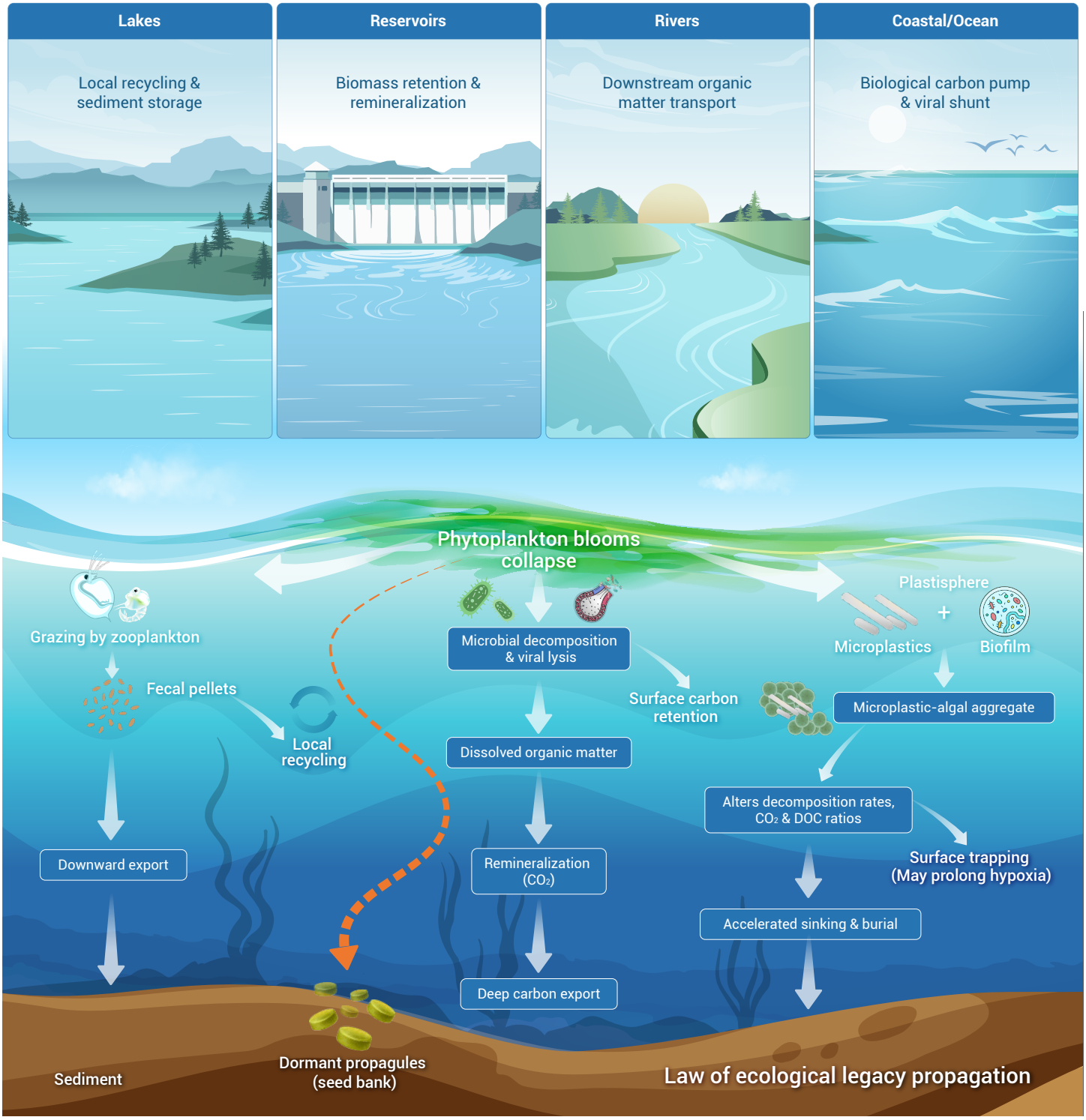

Figure 6. Fate stage across aquatic systems Ecological legacy persists beyond bloom collapse through local recycling and sediment storage in lakes, biomass retention and remineralization in reservoirs, downstream organic matter transport in rivers, and biological carbon pump and viral shunt in coastal and marine systems.

growing interannual variability in Arctic sea-ice dynamics may create increasingly unpredictable persistence windows in the future.[139]

Decline in cryospheric systems is triggered primarily by refreezing rather than nutrient exhaustion, flushing, or viral lysis. When ice reforms, light availability is rapidly eliminated and residual biomass becomes entrained within the growing ice lattice, removing it from the pelagic environment. This mechanism differs fundamentally from sedimentation-driven losses in lakes or advective exports in rivers.[30,47,100] Importantly, ice entrainment can preserve biomass for months or years before release during subsequent melt seasons, creating a delayed recycling pathway with no direct analogue in temperate environments.[131,132]

Rapid mixed-layer deepening and destratification further reduce cumulative light exposure below physiological compensation thresholds, accelerating biomass collapse.[57] Although grazing and viral lysis are major loss processes in lakes and marine systems,[15,16] their roles in cryospheric environments remain comparatively poorly resolved and are likely constrained by lower grazer diversity and shorter ecological interaction times within seasonal melt periods.

The fate of cryospheric bloom biomass diverges most strongly from liquid-water systems through the ice–albedo feedback, unique to ice-covered environments. In lakes, reservoirs, rivers, and oceans, bloom fate is primarily determined by microbial degradation, sedimentation, grazing, or carbon

export.[123] In cryospheric systems, bloom development can leave a physical imprint that persists beyond the lifetime of the bloom itself. Pigmented snow and glacier algae, particularly *Chloromonas nivalis*, darken snow and ice surfaces through carotenoid production, reducing surface albedo by up to approximately 13% over a melt season. Rather than directly sustaining bloom growth, this surface darkening represents a persistent modification of the physical environment. By enhancing local melt, it can increase both the extent and duration of exposed, meltwater-influenced ice, thereby creating surface conditions that may facilitate renewed algal colonization in subsequent seasons.[140] Thus, the fate of cryospheric blooms involves more than biomass loss or export; it can also involve the formation of an ecological legacy—a lasting alteration of the ice surface's energy balance that extends beyond the bloom's immediate life cycle.

Cryospheric blooms also contribute to carbon cycling through rapid particle export and under-ice carbon fluxes. Under-ice diatom blooms support early-season particulate carbon export, while recent shifts from diatom- to cryptophyte-dominated communities alter biological carbon-pump efficiency and propagate through polar food webs.[141] Remote sensing and in situ export measurements further demonstrate that ice-edge blooms can contribute disproportionately to polar carbon sequestration through enhanced mesopelagic carbon transfer following bloom collapse.[88,121]

The cryospheric case study demonstrates that the five-stage bloom life-cycle framework remains broadly transferable across aquatic environments, but the governing controls require substantial reparameterization. Recruitment is controlled by ice-matrix release rather than sediment resuspension, proliferation by light transmission rather than phosphorus or iron availability, persistence by ice phenology rather than nutrient-retention feedbacks, decline by refreezing rather than nutrient exhaustion or flushing, and fate by albedo feedbacks in addition to conventional carbon-export pathways. The cryosphere thus represents a valuable natural experiment illustrating how universal bloom stages persist while the governing mechanisms shift fundamentally across environmental settings.

RESEARCH GAPS AND FUTURE DIRECTION

Despite substantial advances in phytoplankton bloom research, several mechanistic and predictive gaps constrain the development of transferable forecasting frameworks. Critically, these gaps manifest differently across system types and resolving them requires explicitly cross-system approaches rather than system-specific extensions of existing frameworks.

Adaptive phytoplankton plasticity in predictive models

Thermal acclimation, nutrient uptake plasticity, and photoacclimation alter competitive dynamics across all system types, but their effects are expressed through fundamentally different mechanisms.[3,12,25,42,48,64] In lakes and reservoirs, thermal acclimation determines whether cyanobacteria maintain dominance as stratification intensifies under warming.[103] In rivers, plasticity in uptake kinetics governs whether populations can exploit brief nutrient pulses during low-flow windows.[40] In coastal and marine systems, photoacclimation and nutrient flexibility regulate survival during episodic upwelling and mixed-layer deepening events.[25,48] Current models parameterize these traits as fixed values, introducing systematic error when applied across system types. Incorporating dynamic trait-based parameterization, including thermal optima, nutrient acquisition kinetics, and morphology-dependent buoyancy regulation therefore represents a critical step toward improving cross-system bloom prediction.

Life-stage transition thresholds across systems

The environmental thresholds governing bloom stage transitions differ not only in magnitude but also in identity across system types, and this divergence is rarely acknowledged in monitoring design. In lakes, recruitment thresholds are thermal and the relevant timescale is days to weeks.[86] In rivers, bloom initiation can occur within hours of a discharge drop, requiring sub-daily resolution for detection.[7,15] In reservoirs, operational drawdown events can override thermal thresholds entirely, making hydrological event timing the critical monitoring variable rather than temperature.[17] Future monitoring strategies must therefore be system-matched: continuous automated flow cytometry for rivers, daily fluorometry during lake recruitment windows, high-revisit satellite algorithms combined with surface sensors for coastal systems, and autonomous under-ice profilers for cryospheric environments.

Predicting bloom evolution under climate change

Cross-system projections of climate change impacts on blooms remain largely absent. In lakes and reservoirs, warming prolongs stratification and expands recruitment windows, with cyanobacteria projected to dominate under high-emission scenarios.[11,47,113] In rivers, warming combined with increased drought frequency is expected to extend low-flow windows favorable for bloom proliferation.[105] In coastal and marine systems, altered freshwater delivery and nutrient loading are expected to restructure bloom phenology in ways that current models calibrated under historical forcing cannot capture.[142,143] Most critically, interactions between warming and extreme climatic events may normalize bloom conditions even when nutrient targets are met,[113] meaning that cross-system projections must incorporate nonlinear climate feedbacks rather than assuming linear responses to temperature and nutrient gradients.

Hydrological regulation across system types

The influence of hydrological management on bloom dynamics is well documented in reservoirs but remains poorly integrated across other system types. In reservoirs, water-level drawdown and flushing are established bloom suppression tools that operate by reducing residence time and disrupting stratification.[17] In rivers, dam operations control the flow-threshold windows that determine whether recruitment and proliferation are feasible, but the propagation of bloom risk across regulated river networks remains unresolved.[94] In lakes, water residence time determines which loss processes dominate during decline, yet management interventions targeting hydrological retention are rarely incorporated into lake bloom models.[72] Future predictive frameworks must treat hydrological regulation not as a system-specific management tool but as a universal cross-system variable that requires explicit parameterization in all bloom life cycle models.[40,72,144]

Integrated cross-system life-cycle models

The most critical structural gap is that no existing model framework resolves all five bloom life-cycle stages across lakes, reservoirs, rivers, and coastal systems simultaneously. Lake models capture sediment recruitment and internal nutrient recycling but omit advective export.[98] Marine biogeochemical models represent nutrient limitation and stratification-driven proliferation but lack benthic recruitment modules.[104] River models address transport dynamics but omit persistence and fate mechanisms. As a result, bloom biomass, toxins, and organic matter crossing system boundaries through the freshwater-marine continuum cannot currently be tracked mechanistically from source to sea.[4] Developing modular life-cycle architectures that parameterize system-specific controls at each stage transition while sharing a common functional language across systems would substantially improve predictions of bloom transport, toxin export, and biomass fate under changing hydrological conditions. Such frameworks should integrate process-based hydrodynamics, trait-based ecological modules, Bayesian hierarchical calibration, and remote-sensing data assimilation.[98,104]

Toxin regulation across system types

Toxin induction pathways differ fundamentally across system types, and this cross-system divergence remains insufficiently resolved. In freshwater lakes and reservoirs, microcystin production is regulated by nitrogen assimilation, oxidative stress, and carbon allocation pathways, with toxin concentrations frequently decoupled from biomass in ways that complicate risk prediction.[22,63,111] In coastal marine systems, iron limitation activates a distinct cysteine synthase-mediated pathway that produces the BMAA neurotoxin in diatoms, a mechanism entirely absent from freshwater systems.[4] In rivers, rapid advective transport means that even moderate intracellular toxin concentrations may produce ecologically significant downstream exposure through cumulative longitudinal delivery. Future research should integrate transcriptomics, proteomics, metabolomics, and isotope tracing to identify molecular thresholds preceding toxin induction across bloom stages and system types.[22,63,57]

Bloom-associated One Health risks across systems

The One Health risk associated with bloom-driven ARG enrichment varies systematically across system types. In lakes with long residence times, warming restructures bloom-associated microbiomes into persistent ARG hotspots that can remain elevated for weeks after visible bloom decline.[7,116] In reservoirs, operational management that inadvertently extends residence time during warm periods may prolong ARG enrichment windows.[17] In rivers, short residence times limit in situ ARG accumulation but facilitate downstream transport of ARG-carrying bacteria to drinking water intakes, irrigation canals, and aquaculture facilities.[7] Climate warming may further enhance ARG persistence across environmental microbial systems,[99] while bloom-associated microbial consortia can facilitate ARG transfer through aquatic food webs and water infrastructure networks.[7,101] Determining temperature thresholds, persistence dynamics, and post-collapse sediment retention of ARGs across system types represents the most urgent unresolved challenge at the intersection of bloom ecology and public health.

Ultimately, future progress will depend on moving beyond descriptive, comparative ecology toward predictive, management-ready frameworks that integrate trait-based experimentation, high-frequency observations, molecular diagnostics, hydrodynamic forecasting, and cross-system modeling. Such approaches are essential for predicting bloom dynamics under climate change and human hydrological regulation and for translating ecological understanding into operational mitigation strategies. This transition from descriptive synthesis to predictive, mechanistic forecasting represents the next critical step for cross-system phytoplankton bloom science.

CONCLUSION

Most phytoplankton bloom research remains system-specific, which has limited the development of generalizable ecological laws. We synthesized bloom dynamics across lakes, reservoirs, rivers, estuaries, coastal oceans, and cryospheric environments into a unified five-stage life-cycle framework—recruitment, proliferation, persistence, decline, and fate—and uses this framework to compare how each stage is driven by system-specific factors. *Recruitment* is thermally triggered in stratified lakes but typically hydrologically controlled in rivers and reservoirs. *Proliferation* is often co-limited by nitrogen and phosphorus, or nitrogen-limited in freshwaters, generally nitrogen-limited in coastal marine systems, and iron-limited in the open-ocean when nitrogen and phosphorus are replete. *Persistence* involves physiological tolerance and microbiome-mediated buffering, which under warming becomes a hotspot for antibiotic resistance gene enrichment. *Decline* is regulated by residence time: slow-retention systems favor biological losses (viral lysis, grazing), whereas high-flushing systems are dominated by physical export. *Fate* is further modified by plastisphere-associated microbial pathways. The cryospheric case study shows that the framework is transferable after reparameterization (ice-melt release, light transmission, refreezing, albedo feedbacks). Three insights emerge: residence time is a master regulator, bloom-associated microbiomes actively modulate persistence and risk, and life-cycle stages are universal, but thresholds and feedbacks are system-dependent, therefore, transferring models without recalibration introduces predictable errors. Our framework provides a foundation for cross-system bloom prediction and highlights the need for trait-based parameterization, high-frequency observations, and coupled forecasting frameworks.

Table 5. Table of abbreviations.

Abbreviation	Full term
ARG(s)	Antibiotic resistance gene(s)
BMAA	β-N-methylamino-L-alanine
CCMs	Carbon-concentrating mechanisms
CH_4	Methane
polyP	Polyphosphate
CI	Confidence interval
CO_2	Carbon dioxide
CysK	Cysteine synthase
CRISPR/Cas9	Clustered regularly interspaced short palindromic repeats / CRISPR-associated protein 9
2,3-DAP	2,3-diaminopropanoic acid
DIN	Dissolved inorganic nitrogen
DNA	Deoxyribonucleic acid
DO	Dissolved oxygen
DOM	Dissolved organic matter
HAB(s)	Harmful algal bloom(s)
PAR	Photosynthetically active radiation
PSU	Practical salinity unit
ROS	Reactive oxygen species
SOS	SOS response (DNA damage-inducible repair pathway)
N_2	Dinitrogen
UV	Ultraviolet
TP	Total phosphorus

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AUTHOR CONTRIBUTIONS

T.W. & M.J.R. contributed equally to this work. T.W. researched & wrote the manuscript. M.J.R. provided critical guidance, conceptual input, analysis and feedback throughout the study. J.E., Z.W., Z.X., M.Y., P.H-W., B.D.J., Q.B-Q., C.J., S.S and L.Z. read the manuscript and provided constructive feedback. M.X., H.W., & T.K. assisted with the study. All authors contributed to the manuscript and approved the final version.

DECLARATION OF INTERESTS

Erik Jeppesen and Justin D. Brookes are the Editorial Board members of The Innovation Water and were blinded from reviewing or making final decisions on the manuscript. Peer review was handled independently of this member and their research group. The other authors declare no conflicts of interest.

DATA AND CODE AVAILABILITY

No new data were created or analyzed in this study.

SUPPLEMENTAL INFORMATION

It can be found online at https://doi.org/10.59717/j.tiw.2026.100029.