What makes a cyanobacterial bloom disappear? A review of the abiotic and biotic cyanobacterial bloom loss factors

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ABSTRACT

Cyanobacterial blooms present substantial challenges to managers and threaten ecological and public health. Although the majority of cyanobacterial bloom research and management focuses on factors that control bloom initiation, duration, toxicity, and geographical extent, relatively little research focuses on the role of loss processes in blooms and how these processes are regulated. Here, we define a loss process in terms of population dynamics as any process that removes cells from a population, thereby decelerating or reducing the development and extent of blooms. We review abiotic (e.g., hydraulic flushing and oxidative stress/UV light) and biotic factors (e.g., allelopathic compounds, infections, grazing, and resting cells/programmed cell death) known to govern bloom loss. We found that the dominant loss processes depend on several system specific factors including

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cyanobacterial genera-specific traits, *in situ* physicochemical conditions, and the microbial, phytoplankton, and consumer community composition. We also address loss processes in the context of bloom management and discuss perspectives and challenges in predicting how a changing climate may directly and indirectly affect loss processes on blooms. A deeper understanding of bloom loss processes and their underlying mechanisms may help to mitigate the negative consequences of cyanobacterial blooms and improve current management strategies.

1. Introduction

Cyanobacterial blooms, also known as cyanobacterial harmful algal blooms or blue-green algae blooms, have garnered substantial interest from the research community and public health officials due to their negative impacts on water quality (Chorus and Welker, 2021). These impacts include the production of a suite of potent toxins that can cause injury or death in animals and, in rare cases, humans; taste and odor compounds that are difficult and expensive to remove from drinking water supplies; and near-bottom oxygen loss during bloom decomposition that can kill fish and benthic invertebrates (Paerl and Otten, 2013a). Cyanobacterial blooms can disrupt aquatic food webs because these taxa are of relatively poor food quality due to their lack of polyunsaturated fatty acids essential for zooplankton and fish production (Ahlgren et al., 2009; Demott and Müller-Navarra, 1997). There has been mounting evidence suggesting that blooms are increasing globally (Ho et al., 2019; Merder et al., 2023, but see Wilkinson et al., 2021), prompting research in understanding the drivers behind bloom growth and associated toxin production.

Cyanobacterial blooms can be defined as an accumulation of cyanobacterial biomass that causes water discoloration and surface (scums) or subsurface (deep chlorophyll maxima; DCM) aggregations of cells (Giling et al., 2017; Leach et al., 2018; Reinl et al., 2021). Many factors underpin bloom initiation, intensity over time, and geographic expansion. Some of the factors that increase blooms include warming temperature (Kosten et al., 2012; Paerl and Huisman, 2008, but see Reinl et al., 2023), increased water column stability (Visser et al., 2016), increased nutrient inputs (Paerl and Otten, 2013a; Smith, 2003; Smith and Schindler, 2009), changed nutrient stoichiometry (i.e., decreased nitrogen:phosphorus (N:P) ratios; Harris et al., 2014; Orihel et al., 2012; Smith, 1983), altered food web structure (Elser, 1999), presence of persistent organic pollutants and organic nutrient forms (Harris and Smith, 2016; Reinl et al., 2022), and changes in light regimes and the availability of carbon dioxide (Lyche Solheim et al., 2024; Van de Waal et al., 2011). While understanding the causes of bloom formation and toxicity is critically important for prevention and mitigation of cyanobacterial blooms, it is also essential to understand the environmental conditions that lead to the disappearance of cyanobacterial blooms through loss processes.

Both growth limitation and loss processes play a key role in the life cycle of a cyanobacterial bloom, but an important distinction should be made between them (Box 1, Fig. 1). We define a loss process as any process that leads to a reduction of cells from a cyanobacterial population within a defined area or waterbody over a specific timescale (*sensu* Reynolds, 1984; see Box 1). Blooms form when the net cyanobacterial population development is positive, or when the population growth rate exceeds the rate of loss processes occurring at that time (Reynolds, 1984), leading to a visible accumulation of biomass. When the reverse is true and losses override growth, blooms may stop developing and/or accumulation may slow down. The term "limitation" is related to factors that affect the cyanobacterial population growth rate and it happens when there is a deficit in essential growth resources such as light, available carbon and nutrients, and/or temperature (i.e., bottom-up regulation). In contrast, loss processes have a negative impact on the standing stock of biomass, and thus can result in a reduction or reversal of net population development.

Factors that control freshwater and brackish-water cyanobacterial growth (Fig. 1A-C) are the subject of many studies, but relatively little

attention is given to the mechanistic understanding of processes that lead to the loss of cyanobacterial blooms. This is because although loss processes are relatively simple to identify, realistic quantification of specific loss processes are difficult to accurately measure *in situ* and it is challenging to disentangle growth limitation from loss processes (Reynolds, 1984). As a result, there is a paucity of data that legitimately measures the rates and/or magnitudes of specific loss processes, especially for specific loss processes underlying components affecting cyanobacteria taxa. Importantly, contemporary approaches to bloom management focused on loss processes and the compounding effects of climate change have not been explored. To improve our understanding, prediction of cyanobacterial blooms, and water management in general, we need a holistic understanding of cyanobacterial blooms by identifying processes that support bloom growth (Fig. 1A-C) and loss (Fig. 1D-J). In this review, we explore the mechanisms of loss processes in more detail, providing specific examples of cyanobacterial population loss processes in laboratory, mesocosm, field, or modeling studies, as well as review and discuss bloom management approaches to reducing cyanobacterial biomass. Most of the studies we found in the literature were focused on the temperate Northern Hemisphere, indicating a current geographical bias in the literature; however, the study results may be applicable to fresh and brackish water systems in general. We also address potential implications and challenges in determining the effect of loss processes on cyanobacterial blooms now and under future climate conditions.

2. Abiotic loss processes

2.1. Physical transport and dispersion by hydraulic flushing and mixing

Hydraulic flushing or "wash out" of living phytoplankton from a water body or defined area (i.e., flow-connected waterbodies or embayment in larger systems) causes a loss of cyanobacterial cells from the population (Fig. 1D). Hydraulic flushing corresponds to the water residence time and is modulated by floods, droughts, and water management, all of which can indirectly affect other abiotic (turbidity, water column thermal dynamics) and biotic (microbial community composition) conditions that affect cyanobacterial population dynamics (Magalhães et al., 2019). In terms of population dynamics, hydraulic flushing can lead to a net loss of cyanobacterial cells when the physical transport of cells leaving the system are greater than cells entering the system from inflowing water (Reynolds, 1984). Although all phytoplankton taxa are subjected to hydraulic flushing, the relevance of flushing from a system for governing cyanobacterial blooms can be linked to specific cyanobacterial traits. For example, positively buoyant cyanobacterial taxa could be disproportionately flushed from a system relative to non-buoyant eukaryotic algae during relatively calm periods when surface aggregations are present. Subsequently, light winds can transport these scums out of the lake via an outflow or out of an embayment where cells are dispersed in a larger system. In reservoirs, buoyant cyanobacteria can be flushed from surface releases, while mid-water column and near-bottom dam gates may disproportionately flush non-buoyant phytoplankton or cyanobacterial DCMs (Erratt et al., 2022; Lehman, 2014).

Rainfall patterns can have complex effects on cyanobacterial taxa, with the potential for positive and negative influences depending on the intensity and frequency of the event (Anderson et al., 2002; Reichwaldt

and Ghadouani, 2012; Wood et al., 2017). While rainfall events can enhance cyanobacterial growth by increasing nutrient loading, both internally through water column mixing and externally through runoff of surface and subsurface flows (Larsen et al., 2020), high intensity rainfall events can also disrupt water column stratification and cause dilution and flushing to the extent that it reduces and/or causes complete collapse of a cyanobacterial bloom (Jacobsen and Simonsen, 1993; Jones and Poplawski, 1998; Reichwaldt and Ghadouani, 2012). Whether the effect of dilution overrides the nutrient addition effect may likely depend on the trophic status of the water body (Armstrong et al., 2023), and/or colored dissolved organic matter (CDOM) loading, which can affect light critical to cyanobacterial growth (i.e., browning; see de Wit et al., 2016; Lyche Solheim et al., 2024). Maintaining the effects of dilution, however, may require recurrent intense rainfall events (e.g., monsoons; An and Jones, 2000), otherwise nutrient loading and recruitment through increased mixing can restimulate cyanobacterial growth processes.

Lake overturn(i.e., mixing over the full water column depth) can lead to a collapse of gas vesicles, resulting in cyanobacterial biomass loss through activation of programmed cell death/resting cells (section 3.4) and thereby sinking from the water column to the sediments (i.e., sedimentation, Fig. 1E; Walsby, 1994). Overturn, however, under the impact of climate change has become progressively more incomplete (mero- instead of holomixis, Knapp et al., 2021; Mesman et al., 2021), leaving gas vesicles more often intact. While many cyanobacterial species can exploit stratified conditions, flotation through buoyancy does not provide any advantage when turbulent velocities are faster than cyanobacterial flotation rates, keeping cyanobacteria entrained. Additionally, blooms will not develop to the same extent under prolonged windy conditions due to the dispersion of biomass (Ibelings et al., 2003; Paerl and Huisman, 2009). This has been shown in experimental studies where induced mixing resulted in a reduction in nuisance cyanobacterial blooms, while in the absence of mixing, the cyanobacterial blooms reappeared (Lehman, 2014).

Stratification and water column mixing have different effects on cyanobacterial species, with pelagic and benthic life stages responding differently to changes in mixing (Cottingham et al., 2021). For example, studies have shown that filamentous cyanobacteria are negatively impacted by storm-induced turbulence and deep mixing (Moe et al.,

2019; Visser et al., 2016). Some species, however, such as *Planktothrix agardhii* are adapted to these conditions, typically in shallow lakes (Scheffer et al., 1997). Storm-induced mixing events can be strong enough to disrupt stratification, causing a premature loss of actively growing pelagic cyanobacteria if cells are transported below the compensation depth, resulting in gas vesicle collapse. If gas vesicles collapse repeatedly under combined turgor and hydrostatic pressure, cells are no longer able to control their buoyancy and sink to the sediment (Huisman et al., 2004; Kinsman et al., 1991; Visser et al., 1996; Walsby, 1994). Conversely, cyanobacterial benthic stages can take advantage of increased mixing, by returning to the water column via germination and active recruitment, or though passive recruitment via physical resuspension by sediment mixing or ebullition (Cottingham et al., 2021; Slavin et al., 2022 and references therein). Storm-induced upwelling of DCM forming cyanobacteria in deep lakes can lead to a surface bloom formation (Giling et al., 2020; Reinl et al., 2023). Understanding the complete cyanobacterial life cycle (including pelagic and benthic phases) of species and even strains, and the net effects of these potentially counteracting abiotic processes (stratification and mixing) are essential to predict future cyanobacterial loss process dynamics.

2.2. Oxidative stress and UV light

The primary energy source for photoautotrophic organisms such as cyanobacteria is photosynthetically active radiation (PAR; wavelengths between 400-700 nm; Rastogi et al., 2014). Photoautotrophic organisms produce reactive oxygen species (ROS) as a byproduct of photosynthesis, which can cause oxidative stress whenever the overproduction of ROS occurs (i.e., more than can be handled by photoprotective defense mechanisms). Oxidative stress can be toxic for cells and lead to cell death (Fig. 1F). Light also plays an important role in the formation of ROS, with high amounts of UV light promoting the overproduction of ROS. Besides reactive radicals such as the superoxide anion (O_2^-) and the hydroxyl radical (OH^-), the non-radical oxidant hydrogen peroxide (H_2O_2) is another important ROS form. Contrary to eukaryotes, which can produce H_2O_2 under high light stress in a process called the Mehler reaction, cyanobacteria cope with high light stress in a Mehler-like response that does not produce H_2O_2 and may therefore be more
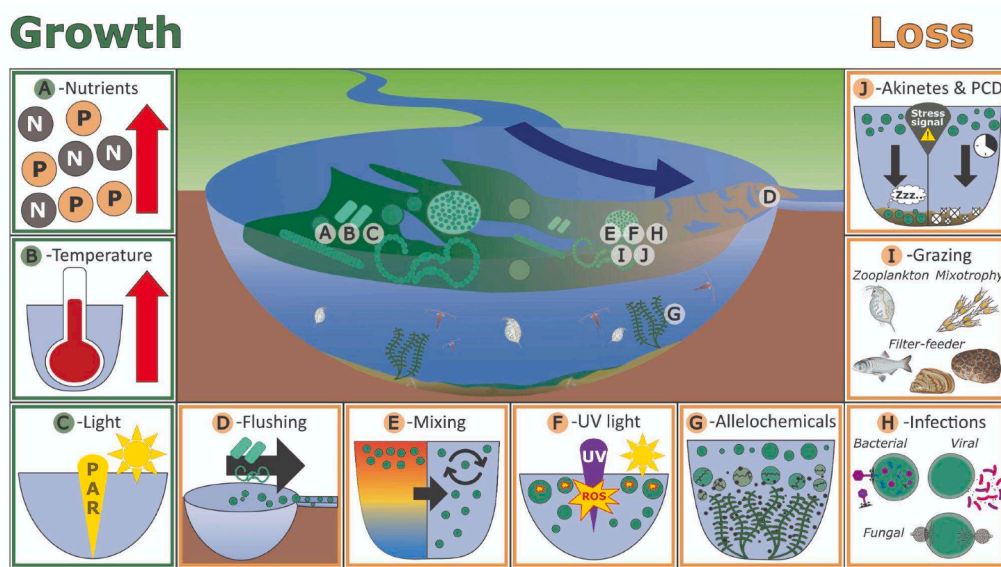
Fig. 1. Growth (left, green letters) and loss (right, brown letters) processes that contribute to observed cyanobacterial blooms in aquatic systems. Growth processes include (A) nutrients, (B) temperature, (C) light, and loss processes include (D, E) hydraulic flushing and water column mixing, (F) UV light damage, (G) allelochemicals, (H) infections, (I) grazing by zooplankton, mixotrophs, and other filter-feeders, and (J) akinetes and programmed cell death (PCD). Subsurface and benthic blooms (not shown) are affected by the same processes as planktonic blooms.

sensitive to relatively high H_2O_2 levels (Piel et al., 2019). For example, experiments comparing the response of cyanobacteria and green algae (Leunert et al., 2013) revealed that *Microcystis aeruginosa* was affected at substantially (2 orders of magnitude) lower H_2O_2 concentrations compared to green algae. The combination of UV irradiation and colored dissolved organic matter (CDOM) resulted in H_2O_2 concentrations of 1.5 $\times$ 10^{-7} M to 3.6 10^{-7} M indicating inhibition of cyanobacterial photosynthesis by UV-irradiated CDOM, but not of green algae. These findings demonstrate that phytoplankton community composition and activities are controlled by UV generated ROS, in particular, H_2O_2. Research has suggested, however, that microcystins may protect cells against oxidative stress caused by relatively high ROS (Paerl and Otten, 2013b; Švanys et al., 2016; Zilliges et al., 2011), meaning that cyanobacterial cells may have adapted to harmful oxidative stress conditions to lessen the loss process of photooxidative death.

Ultraviolet radiation (UVR), which represents UV-A (315-400 nm), UV-B (280-315 nm), and UV-C (100-280 nm), can result in physiological damage to cells that causes cell death. Solar UV-B radiation has been shown to have negative effects on cyanobacteria, affecting their growth, pigments, enzymatic processes, buoyancy, DNA, and protein structure (Rastogi et al., 2014; Sinha et al., 2001). The loss effects of UV-B on cyanobacteria populations depend on the amount of radiation exposure and species/strain specific traits such as morphological shape and outer membrane sheaths, ability to produce mycosporine-like amino acids (i. e., "sunscreen" compounds), and efficiency in post-exposure DNA repair (Rastogi et al., 2014). For example, Zeeshan and Prasad (2009) found that the colonial *Aphanothece* sp. was less sensitive to UV-B radiation compared to *Plectonema boryanum* and *Nostoc muscorum*, possibly

because colonial morphologies may help reduce UV-B radiation effects like photobleaching of photosynthetic pigments. El-Sheekh et al. (2021) found differential growth, pigment, and cellular structure responses between five phytoplankton taxa exposed to UV-B, including significant differences between freshwater and marine *Microcystis* sp., which indicates that responses to UV-B may depend on strain-level differences within a single species. Zhang et al. (2013) showed that regardless of toxin capability, *Microcystis aeruginosa* strains were unable to outcompete the Chlorophyte *Chlamydomonas microsphaera* in competition experiments with UV-B radiation exposure. Thus, UV-B radiation can alter the phytoplankton community composition, including within cyanobacterial populations with multiple species/strains.

Photobleaching of cyanobacterial photosynthetic pigments has also been observed under UV-B radiation exposure. Donkor and Häder (1996) observed that phycobilins (the major accessory pigments of cyanobacteria) were bleached first, followed by carotenoids. A reduction of *Nostoc muscorum* pigments occurred after 35 minutes of UV-B exposure, and after 70 minutes, phycocyanin, carotenoids, and chlorophyll *a* were reduced by more than 75 % (Agrawal, 1996). For the rice-field cyanobacterium *Trichormus fertilissimus* (formerly *Anabaena fertilissima*), 2-3 hours of UV-B radiation exposure completely bleached all pigments (Banerjee and Häder, 1996), causing programmed cell death. Other studies have found UV-B causes pigment photobleaching in *Dolichospermum* sp. (formerly *Anabaena*; Gao et al., 2007), *Microcystis* sp. (Babele et al., 2017; Jiang and Qiu, 2011), and *Planktothrix* sp. (El-Sheekh et al., 2021), showing that UV-B radiation can cause loss processes in globally important bloom-forming taxa. Although prolonged exposure to UV-B causes photobleaching in cyanobacterial cells,

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Box 1

The difference between growth limitation and loss processes is clearly illustrated in the modeling literature. Reynolds (1984) compartmentalized loss processes into hydraulic washout, sedimentation, grazing, and death. This was represented by the following equation:

$$K^{'} = K_n + K_l \tag{1}$$

where K' is the specific growth rate, K_n is exponential growth, and K_l are exponential loss processes. Reynolds (1984) states "In terms of population dynamics, [loss] is any process which actively removes biomass from the part of the water body under consideration and therefore depletes the potential stock of growing organisms. To some extent, they are all instantaneously density dependent and can be expressed in the same rate terms as growth (i.e., in fractional or natural log units):

$$\frac{\delta N}{\delta t} = e^{k_n} = e^{(k^{'} - \Sigma k_L)} \tag{2}$$

where N is the population of cells, t is time, and k_n, k', and $\sum k_L$ are respectively the exponential rate constants of net change, growth, and the summed losses." Reynolds (1984) further defines $\sum k_L$ as the sum of k_w (washout), k_s (sedimentation), k_d (death), and k_g (grazing). Resource limitations (i.e., temperature, light, and nutrients) are not included in the loss process term.

Similarly, Chapra (2008) states that "In nature such levels [of hypothetical maximum biomass] are never reached, along with growth, there are a number of loss processes. Some of these are transport-related such as settling and diffusion/dispersion. Others are kinetic, e.g., respiration, excretion, and death by predation. Further, the growth rate itself is not a simple constant, but varies in response to environmental factors such as temperature, nutrients, and light. At low levels, and in some instances at high levels, these factors can limit growth". Chapra (2008) presents biomass concentration as a function of time as:

$$\frac{da}{dt} = k_g(T, N, I)a - k_d a \tag{3}$$

where *a* is algal biomass concentration, t is time, $k_g(T, N, I)$ is growth rate as a function of temperature (T), nutrients (N), and light (I), and k_d is the loss rate. Chapra (2008) then expresses the growth rate as:

$$k_g(T, N, I) = k_{g,T}\phi_N\phi_L \tag{4}$$

where $k_{g,T}$ is the maximum growth rate at a given temperature under saturated light and nutrient conditions, and ϕ_N and ϕ_L are nutrient and light limitation factors that vary between 0 and 1.

These mathematical expressions of growth and loss presented in past efforts and here demonstrate that resource limitations act on growth and are separate from loss processes (but see section 3.4). Here, we define growth and loss processes equivalently to Reynolds (1984) and Chapra (2008) but compartmentalize the loss processes into abiotic and biotic factors that actively remove cyanobacterial cells from a population.

Jiang and Qiu (2011) showed that short (<2 hours) exposures cause pigments to initially increase in *Microcystis aeruginosa*, indicating that UV-B exposure time needs to be prolonged to cause loss in cyanobacterial populations.

When buoyant cyanobacteria (e.g., *Microcystis* sp. and *Dolichospermum* sp.) float to the lake surface, they may be exposed to extreme conditions, such as intense UV radiation and temperatures exceeding cellular thermal thresholds. When surface blooms accumulate in dense surface scums (e.g., by horizontal transport of the initial surface bloom to the leeward shore), the local C demand increases, all available C (e.g., CO_2 and HCO_3) is fully depleted, and pH values may rapidly increase to 10-11 (Ibelings and Maberly, 1998). While C demand limits the population growth rate, elevated pH values increase the likelihood of photooxidation death as a loss process in cyanobacterial scums (Abeliovich and Shilo, 1972; Shapiro, 1973). Thus buoyancy, although being a key trait in promoting growth of bloom forming cyanobacteria, has a trade-off and may contribute to substantial biomass losses. If prior to surface bloom formation, cyanobacteria were subjected to deep mixing and experienced low PAR, they will lack the necessary photoprotection from carotenoids like zeaxanthin (Ibelings et al., 1994). Walsby et al. (1991) showed this was the case for *Anabaena* (now *Dolichospermum*) *lemmermannii* in Lake Windermere, where during an extended period of relatively low irradiance, cells overinvested in new gas vacuoles and subsequently were unable to lose buoyancy through ballast accumulation. In turn, this caused cells to be stuck at the surface, exposing them to harmful levels of oxidative stress and UV radiation that induced photoinhibition and eventually cell loss due to photooxidative death.

3. Biotic loss processes

3.1. Allelochemical compounds

Allelochemicals are chemical compounds produced by many terrestrial and aquatic organisms and can have either positive or negative impacts on other organisms. Allelochemicals that affect cyanobacterial blooms are produced by various organisms including macrophytes, heterotrophic bacteria, fungi, phytoplankton, and terrestrial plants (B. Li et al., 2021). Allelochemical compounds secreted by macrophytes have been shown to disrupt photosynthetic pathways in *Microcystis aeruginosa* by destroying pigment content of phycobilisomes (J. Li et al., 2021) , inhibiting photosystem II (PSII) activity, and blocking electron-transfer between PSI and PSII (Zhu et al., 2010), all of which ultimately block cell access to stored materials and energy and can lead to cell death (Fig. 1G). Studies examining the effects of polyphenolic compounds, such as allelopathic chemicals secreted by the aquatic vascular plant *Myriophyllum spicatum* on *M. aeruginosa* and *Limnothrix redekei,* have also shown strong detrimental effects on the physiology and growth of cyanobacteria (He et al., 2016; Hilt et al., 2006; Jeong et al., 2021; Lu et al., 2017; Švanys et al., 2014). Allelochemical compounds are also able to induce cell death directly. These compounds may trigger oxidative stress in cyanobacteria, resulting in the production of ROS (Hong et al., 2011). For example, pyrogallic acid produced from Eurasian watermilfoil (*Myriophyllum spicatum*) stimulated production of ROS, which was shown to lyse cell membranes and break DNA in *M. aeruginosa* (Wang et al., 2017; Wu et al., 2011).

Not all cyanobacteria species display equivalent levels of sensitivity to allelochemicals released by macrophytes (Hilt and Gross, 2008). While *Oscillatoria* sp., *Dolichospermum* sp., and *Microcystis* sp. are highly sensitive to a wide range of macrophyte allelochemicals (Korner and Nicklisch, 2002; Mulderij et al., 2005), species of *Planktothrix* (*P. agardhii* and *P. rubescens*) have been shown to resist allelopathic activities of some macrophytes, such as *Chara* sp. (Berger and Schagerl, 2003). Different genetic strains within the same cyanobacterial species have even been shown to have differential responses to allelopathic influences (Eigemann et al., 2013). For instance, toxin producing strains of *M. aeruginosa* can withstand macrophyte allelochemicals better than

the non-toxin producers (Liu et al., 2007; Mulderij et al., 2005; Švanys et al., 2016; Wu et al., 2011). Thus, cyanobacterial community composition can impact the extent of allelopathic influence and vice versa - cyanobacterial biomass loss due to allelochemicals could be more pronounced in non-toxigenic blooms, while systems rich in anti-cyanobacterial allelochemicals could select for toxigenic strains of cyanobacteria.

Certain bacteria are constitutive or induced to produce cyanobacteriocidal compounds, causing cell lysis and death (Coyne et al., 2022). Bacteria can also produce cyanobacteriocidal compounds to inhibit cell growth (Coyne et al., 2022). Manage et al. (2001) showed that aside from cyanophages, the cyanobacteriocidal bacterium *Achromobacter denitrificans* was significantly, negatively correlated to *M. aeruginosa* biomass, indicating that this bacterium may help decompose *M. aeruginosa* blooms. Fungal allelopathy can also cause cyanobacterial population loss in lakes, and their capability to cause cell death may be dependent on the coevolution between fungi parasites and specific cyanobacterial hosts. Fungal species produce allelopathic compounds that target common bloom-forming cyanobacterial taxa. Jin et al. (2018) reported that the concentration of superoxide anion radical (O_2^-), which can damage the sulfhydryl group of the cell membrane and cause cell death (see section 2.2), increased in media after exposing *M. aeruginosa* to 3,4-dihydroxybenzalacetone sourced from fungi taxa *Phellinus noxius* HN-1. Similarly, 15 fungal species belonging to Ascomycetes (9) and Basidiomycetes (6) have been reported to inhibit and lyse cyanobacteria including *Microcystis, Dolichospermum, Anacystis*, and *Oscillatoria*, and 6 species (3 of which also lyse cells) degraded microcystin-LR (Mohamed et al., 2021). The reported fungus-cyanobacterium interactions were mostly indirect (no direct cell-to-cell contact), and some of the lytic enzymes and other compounds released by fungi selectively damaged the cells of the target cyanobacterium, while the co-occurring eukaryotes were unaffected. These cyanobacteriocidal fungi were sourced mostly from lakes and reservoirs, while some originated in soil and decomposing organic matter (Mohamed et al., 2021).

Phytoplankton can also produce allelochemicals for interference competition with other species. Arii et al. (2015) found that the volatile organic compound β-cyclocitral produced by *Microcystis* sp., initiates lysis of other cyanobacterial taxa cells. In two Japanese lakes, species of *Dolichospermum* and *Aphanizomenon* disappeared after β-cyclocitral was released from *Microcystis*, resulting in *Microcystis* dominance. They also demonstrated that the β-cyclocitral damages the cells of other cyanobacteria species, leading to cell death. A study by Sedmak et al. (2008) highlights the potential for "non-toxic" cyclic peptides that are formed by bloom-forming cyanobacteria to cause cyanobacterial bloom collapse. The cyclic peptides planktopeptin BL1125, anabaenopeptin B, and anabaenopeptin F were extracted from *Planktothrix rubescens* cultures and added to non-axenic *M. aeruginosa* cultures. *Microcystis* cells were inhibited by virus-like particles and behaved like a host. Consequently, these lysogenic cells, when the cyclic peptides are present, promote release of infectious virus-like particles that can cause rapid cyanobacterial bloom collapse via cell death. Experimental work showed the effect of periphyton biofilm on a bloom of *Microcystis,* demonstrating the strong inhibitory effects of indole and 3-oxo-α-ionone, allelopathic chemicals produced by biofilms dominated by diatoms including *Synedra ulna* Kütz., *Gomphonema parvulum* Kütz., *Fragilaria vaucheriae* Kütz., *Melosira varians* Ag., and *Nitzschia amphibia* Grun. These compounds caused cyanobacterial death by damaging the light harvesting structures and disrupting electron transport during photosynthesis (Wu et al., 2011).

Among the compounds produced by cyanobacteria, cyanotoxins have also been explored for their potential allelopathic effects on competing phytoplankton, including other cyanobacteria. Although the mechanisms are not yet well-described, harmful effects of cyanotoxins on other cyanobacteria appear to be related to oxidative stress under laboratory conditions (Dziallas and Grossart, 2011; Leflaive and

Ten-hage, 2007). For example, the production of microcystin-RR elevated levels of ROS and malondialdehyde in *Synechococcus elongatus* (Hu et al., 2005), and microcystin-LR induced cell lysis and reduced nitrogenase activity in *Nostoc* and *Dolichospermum* (formerly *Anabaena*; Singh et al., 2001). How these effects play out under natural conditions, with mixed phytoplankton assemblages and the potentially complex assortment of compounds being released, is currently unknown (Leflaive and Ten-hage, 2007).

Compounds derived from terrestrial plants have also been shown to have allelopathic effects on cyanobacterial taxa. For example, Neilen et al. (2020) found that leachate compounds like proline from river oak (*Causuarina cunninghamiana*) and gallic acid and polyphenols from forest red gum (*Eucalyptus tereticornis*) trees were phytotoxic to *Raphidiopsis raciborskii* in laboratory incubations. In a subsequent 10-day in-reservoir mesocosm experiment, Burford et al. (2022) showed that leachate compounds including fatty acids, sugars, and gallic acid from *E. tereticornis* can have allelopathic effects on *R. raciborskii* blooms that cause loss, even though relatively low treatment concentrations of leachate compounds did not significantly alter light attenuation and increased organic nutrients. Thus, while evidence exists that terrestrial derived organic matter (leachate) can cause direct cyanobacterial loss via allelopathy, more research is needed to define specific compounds from terrestrial plants and specific conditions that could cause allelopathy in cyanobacterial assemblages.

3.2. Infections

3.2.1. Bacterial

There is a symbiotic relationship between heterotrophic bacteria and cyanobacteria (e.g., (Woodhouse et al., 2018 and references therein). Cyanobacteria shape their associated bacterial community composition (Cook et al., 2021), and several studies have reported the mechanisms by which heterotrophic bacteria influence cyanobacterial population dynamics in aquatic systems (Sun et al., 2018). Osman et al. (2017) identified several bacterial antagonists on several cyanobacterial species, and later observations by Le et al. (2022) showed a strong cyanobacteriocidal effect of a variety of heterotrophic bacteria on *M. aeruginosa* (Fig. 1H). Le et al. (2022) also report on the population growth inhibition of *M. aeruginosa* by various heterotrophic bacteria. In controlled laboratory settings, lytic bacteria and those with the ability to degrade microcystin, increased in abundance during the last stages of cyanobacteria blooms (Omidi et al., 2021); however, specific mechanisms for how cyanobacteriocidal bacteria cause cell death in *in situ* blooms is still unclear.

3.2.2. Fungal

Fungal and fungal-like parasites (i.e., true fungi and Oomycota) have the potential to infect - and lyse - cyanobacterial cells, resulting in population loss (e.g., Canter and Lund, 1948; Frenken et al., 2017). Chytrids are frequent and important fungal parasites of large phytoplankton such as filamentous cyanobacteria (Frenken et al., 2017; Gerphagnon et al., 2015). Chytrids are characterized by a motile stage, called zoospores, which swim out from mature sporangia developed on infected phytoplankton hosts including cyanobacteria, and use chemotaxis to find, attach, and infect new hosts (Gleason et al., 2015). Often, but not always, new infections eventually cause the death of the cyanobacterial host, resulting in a loss of cyanobacterial cells from the bloom population. Chytrids are often highly host specific at the species, or even strain level (Sønstebø and Rohrlack, 2011). This contributes to the maintenance of the genetic and phenotypic diversity of cyanobacterial populations (Gsell et al., 2013; Rohrlack et al., 2015) through so-called "Red Queen" dynamics (or negative frequency dependent selection). Chytrid epidemics, characterized by an expansion of infection prevalence, are often concurrent with bloom periods of their hosts. Blooms have clear advantages for the spread of parasites, as transmission from an infected cell to a new host is far easier when the host cell

density is relatively high. If cyanobacterial hosts can develop a bloom before chytrids are able to start infecting cells, the bloom is allowed to reach higher density, and is therefore, followed by a more extreme prevalence of infection (Ibelings et al., 2011). In other words, the longer the delay between the start of the bloom and the onset of infection, the higher the prevalence of infection.

Abiotic lake conditions play key roles in the level of infection that is attained, exclusive of host cell density. Rohrlack et al. (2015) and Wierenga et al. (2022) studied infection of *P. rubescens*, modulated by gradients of both temperature and light, as well as their interaction. These studies provide evidence for how the cyanobacterium's metal-imnetic habitat - relatively dark and cold conditions - protects the host from high levels of chytrid infection. Chytrids specializing in infection of akinetes or heterocysts have been described (Gerphagnon et al., 2015). Experiments have shown that heterocyst infections only lead to strong host population losses in the absence of a N source like ammonium, because the cyanobacterium would then be forced to rely on N_2-fixation by its infected, and therefore dysfunctional, heterocysts.

3.2.3. Viral

Cyanobacterial phages can infect and kill cyanobacteria cells (Bergh et al., 1989; Proctor and Fuhrman, 1990). Cyanobacterial phages are thought to be strain specific, targeting a wide range of host species including heterocyst-forming (*Dolichospermum, Nostoc*) and non-heterocyst-forming filamentous forms (*Lyngbya, Phormidium*, and *Plectonema*), unicellular (*Synechococcus, Anacystis*), and colonial (*Microcystis*) cyanobacterial taxa (Grasso et al., 2022 and references herein). Virus-like particles usually follow the seasonal patterns of their hosts and chlorophyll *a* was found to be a good predictor of viral abundance (Maranger and Bird, 1995). Accordingly, virus-like particles were linked to the collapse of filamentous cyanobacteria species (*Oscillatoria cf. limnetica* and *Prochlorothrix hollandica*) in laboratory-scale enclosures (Gons et al., 2002), and to sharp declines in *M. aeruginosa* populations in lakes (Xia et al., 2013). Likewise, in a co-culturing experiment with natural viral populations and *Microcystis* isolates, phage densities showed a high correlation with the host's cell lysis and within 6 days, causing *Microcystis* abundance to decrease by 95 % (Tucker and Pollard, 2005).

Viral infections can also affect the physiology and metabolism of cyanobacteria, which can lead to programmed cell death. Jiang et al. (2019) observed that viral infection inhibited photosynthesis and reduced the mechanical stiffness of the membranes of *Microcystis* isolates. Several studies have brought up the potential of phages as a potential strategy to control cyanobacteria blooms (Bhatt et al., 2023; Grasso et al., 2022). Nevertheless, the research on this topic remains in its infancy and its feasibility to control cyanobacterial populations under real-life scenarios needs further exploration. This is mainly because phage-sensitive cyanobacteria are a small fraction of the population and the extension of blooms pose serious practical restrictions on the application of this method (Rong et al., 2022; Wilson et al., 1996; Yoshida et al., 2006). For example, Waechter et al. (2019) estimated that to control a bloom as observed in Lake Okeechobee in 2016 (Kramer et al., 2018), it would require 1.2×10^9 liters of phage stock, and viral lysis may lead to the massive release of toxins, as was the case after a *Microcystis* bloom near the water intake during the 2014 water crisis in Toledo (USA; McKindles et al., 2020).

3.3. Grazing/Herbivory

3.3.1. Zooplankton

Consumption of bloom forming cyanobacteria by planktonic and benthic herbivores is a primary loss factor controlling cyanobacteria population dynamics (Fig. 1I), though cyanobacterial traits such as toxins, the absence of polyunsaturated fatty acids required for herbivore growth, and morphological defenses (colony or filaments) often reduce grazing loss. Cladocerans, copepods, and rotifers are taxonomic groups

that dominate zooplankton abundance and biomass of multicellular zooplankton in fresh and brackish waters globally, although tunicates (e. g., salps) and larval phases of benthic organisms are also abundant in marine waters.

Cladocerans, especially large body organisms such as *Daphnia* species, have the highest potential to graze down cyanobacterial blooms due to the combination of traits this genera possesses (De Meester et al., 2023); several studies have revealed their potential to control cyanobacterial blooms in temperate systems. For instance, Chislock et al. (2013) demonstrated that, despite high initial cyanobacteria and microcystin levels, locally adapted *Daphnia pulicaria* populations previously exposed to *Microcystis* were able to grow rapidly and reduce phytoplankton biomass by 70 % to 80 % in hypereutrophic ponds in Alabama and Michigan, USA. Similarly, Lange et al. (2023) found that experimental *Daphnia magna* populations can adapt to a toxic *Microcystis* strain isolated from the same location, suggesting their potential to control blooms via grazing. However, trophic cascades may reduce *Daphnia* biomass due to increased fish predation (Carpenter et al., 1985). Studies have also found that the interaction between cyanobacteria and zooplankton is complex and factors such as genotypes and coevolution of cyanobacteria and *Daphnia* (Lemaire et al., 2012) and grazing traits of zooplankton (selective vs. generalist; Ger et al., 2016) can enhance or reduce the effect of grazing on cyanobacterial abundance. For example, a positive relationship between cyanobacteria and zooplankton, particularly with daphnid and copepod biomass, was observed in a 640-lake data set spanning 12 ecozones in Canada to identify the drivers of cyanobacteria biomass (MacKeigan et al., 2023).

Planktonic copepods (e.g., calanoid and cyclopoid) often dominate zooplankton biomass instead of *Daphnia* in freshwater, brackish, and marine waters (De Meester et al., 2023). Copepods use active selective grazing and have relatively large prey size compared to their body size (Hansen et al., 1997); however, they generally do not cause cyanobacteria population loss to the same extent as larger zooplankton taxa like *Daphnia* (but see Haney, 1987). Copepods use chemosensory cues to select and ingest the most nutritious prey particles available, while individually handling and rejecting harmful, toxic, inedible, or nutritionally inferior particles (Kiørboe, 2011; Rangel et al., 2020). For example, copepods are not known to graze significantly on *Microcystis*, either in experiments with unicellular cultures (Ger et al., 2016) or colonies in natural aquatic systems (Ger et al., 2018; Sellner et al., 1993). In general, the grazing potential for cyclopoid copepods is less than calanoids due to their lower mass specific ingestion rate and raptorial grazing mode (Kiørboe, 2011). Overall, copepods are not a strong candidate for cyanobacterial population loss via grazing, although locally adapted populations from the genus *Notodiaptomus* (neotropics) and *Eurytemora* (Baltic Sea), among others, may graze on toxin producing filamentous cyanobacteria such as *Raphidiopsis* and *Nodularia*, respectively, in the absence of more nutritious prey (Hogfors et al., 2014; Leitão et al., 2021; Novotny et al., 2023). Yet, calanoid copepods that are tolerant to cyanobacterial toxins are also known to ingest significant amounts of filamentous cyanobacteria, especially when alternative nutritious prey is limited (Hogfors et al., 2014; Leitão et al., 2021). For example, new methods such as metabarcoding showed that cyanobacteria, despite assumed low nutritional value for copepods, were detected in all copepod samples in a tidal freshwater reach of the San Francisco Estuary, California (Holmes and Kimmerer, 2022). Although copepods are not strong herbivore candidates for cyanobacterial population control, their role in phytoplankton community structure is complex in that they can cause cyanobacteria loss through grazing, or support cyanobacterial dominance through grazing preference for other eukaryotic species, or help relieve phosphorus limitation of cyanobacterial populations via P excretion (Ger et al., 2019; Hong et al., 2015; Leitão et al., 2021, 2018).

Apart from the larger crustacean zooplankton like cladocerans and copepods, smaller sized rotifers occur in many aquatic systems as well (Sweeney et al., 2022). Despite their relatively small body sizes, they can be important grazers under conditions of poor or low food quality, such as during cyanobacterial blooms (Stemberger and Gilbert, 1985). For example, Kâ et al. (2012) suggested that *Keratella* sp. from the Senegal River (in West Africa) grazed upon filamentous cyanobacteria taxa (*Dolichospermum* sp.) and significantly reduced their abundance in a laboratory grazing experiment. In field observations, however, the consumption rate of rotifers on cyanobacteria were much lower than that on other phytoplankton taxa, and rotifers did not effectively impact cyanobacteria biomass (Sellner et al., 1993). In contrast, the rotifer genus *Keratella* showed a preference for filamentous cyanobacteria (*Nostocales*) during a summer bloom in the Baltic Sea and contributed substantially to cyanobacteria losses together with small cladocerans of the genus *Bosmina* (Novotny et al., 2023). Other studies revealed that rotifers, e.g., *Brachionus calyciflorus* and small cladocerans such as *Bosmina longirostris,* fed selectively in mixtures of colonial *M. aeruginosa* and the nutritious green alga *Chlamydomonas reinhardi* (Fulton and Paerl, 1988).

3.3.2. Fish

Fish can play a significant role in grazing cyanobacteria, both through the direct effects of grazing as well as indirectly through cascading effects by increasing the grazing pressure of zooplankton. This indirect effect of fish through changing the ratio of piscivorous to zooplanktivorous fish has been applied in a widely used shallow lake management strategy coined biomanipulation, with success varying depending on the intensity of fish reduction (Meijer et al., 1999), and the complexity or degree of omnivory in the food web (Elser, 1999).

The impact of fish grazing on cyanobacterial population dynamics, however, varies with fish species, cyanobacterial species, and bloom toxicity. In a biomanipulation experiment using mesocosms filled with Lake Taihu water, filter-feeding silverhead or bighead carp were added to mesocosms with an aim of controlling cyanobacteria through direct grazing. Mesocosms containing only silverhead carp had a higher success rate at lowering cyanobacterial biomass than mesocosms with only bighead carp due to the ability of silverhead carp to graze relatively smaller cyanobacterial taxa like *Microcystis* compared to relatively larger cyanobacterial taxa like *Dolichospermum* (Yi et al., 2016). Another study evaluated the efficacy of cyanobacterial biomass removal through direct grazing from silverhead and bighead carp, and also demonstrated that these fish species could significantly reduce biomass with no change in zooplankton abundances, indicating that the impacts were due to direct herbivory and not trophic cascade processes (Xie and Liu, 2001). Tilapia (*Oreochromis niloticus*) has also been studied for impacts of cyanobacterial toxins on grazing (Beveridge et al., 1993; Keshavanath et al., 1994). In both studies, grazing was higher on non-toxic strains, and Beveridge et al. (1993) also found that fish that ingested the non-toxic strains were healthier than those that ingested toxic strains of *Microcystis*. Although top-down trophic cascades are typically employed to use fish to remove phytoplankton blooms, these studies show that filter feeding fish can also have a direct impact on cyanobacterial population dynamics through grazing.

3.3.3. Mussels and other filter feeders

Filter feeders such as mussels and bryozoans can have a strong influence on planktonic species distribution through grazing. Although many mussel species can filter cyanobacterial cells from the water column (e.g., Silva et al., 2020; Silva and Giani, 2018), the strongest effects on phytoplankton and especially cyanobacteria communities can be attributed to Dreissenid mussels (Zebra mussel/*Dreissena polymorpha* – Quagga mussel/*Dreissena bugensis*); a family of mussels that are invasive in Europe and North America. Yet, the impact of the rise in Dreissenid abundance on cyanobacteria population dynamics varies, possibly due to the trophic state of the water bodies and the composition of the phytoplankton community (Feniova, 2020). A meta-analysis on freshwater systems has shown that overall phytoplankton abundances were significantly reduced by 35 % to 78 % after Dreissenid invasion (Higgins

and Vander Zanden, 2010). A strong decline in cyanobacteria abundances of up to 58 % has been shown after dreissenid invasion in several studies (Kirsch and Dzialowski, 2012; Knoll et al., 2008; Nicholls et al., 2002; Reynolds and Aldridge, 2021), with the strongest declines in species of *Aphanizomenon* (Reynolds and Aldridge, 2021) and *Dolichospermum* (Knoll et al., 2008). On the other hand, several studies found a post-invasion increase of certain cyanobacteria species, in particular of *Microcystis* sp. (Knoll et al., 2008; Nicholls et al., 2002; Raikow et al., 2004; Vanderploeg et al., 2001). Several reasons might explain these findings. Lab experiments show highly species-selective clearance rates of Dreissenids on individual cyanobacteria, including colonial or toxic strains (Dionisio Pires et al., 2005; Tang et al., 2014; Vanderploeg et al., 2001). Grazing experiments revealed that zebra mussels cleared a toxic strain of *P. agardhii* at a higher rate than a non-toxic *P. agardhii* strain (Dionisio Pires et al., 2005). Vanderploeg et al. (2001) suggested a selective feeding/rejection mechanism of zebra mussels through excretion of *M. aeruginosa* in pseudofeces. Although the reasons for the selectivity of mussels are still under debate, taxa, cell size, cell morphology, colony formation, and toxicity seem to be the most decisive properties. Filtration by mussels often results in ejection of cyanobacteria as agglomerated pseudofeces, rather than assimilation through effective ingestion (Dionisio Pires et al., 2007, 2005), resulting in increased sedimentation rates (i.e., via programmed cell death) and thus removal from the water column (Klerks et al., 1996).

While less-studied than mussel filter feeders, bryozoans are aquatic invertebrates that can ingest cyanobacteria along with other suspended particles by filter-feeding (Wood, 2019). In freshwaters, they can form large colonies that appear as gelatinous masses (e.g., brain-like) or tubular branches. Because cyanobacteria can be physically transported downwind into leeward shores, bryozoans growing in areas downwind of blooms are capable of filtering cyanobacteria from the water column (grazing); however, studies examining bryozoans impact on cyanobacterial loss are currently lacking in the literature.

3.3.4. Mixotrophic algae, bacteria, ciliates, and protists

Mixotrophic algae, or algae that perform photosynthesis as well as cell grazing for a C source, can also contribute to population loss of cyanobacterial blooms. Mixotrophic phytoplankton compete with cyanobacteria for abiotic resources like light and nutrients, but also influence cyanobacteria densities through grazing (Wilken et al., 2014). The presence of certain chrysophytes has been associated with cyanobacterial bloom loss, especially mixotrophs like the chrysophyte *Ochromonas* sp. For example, *Ochromonas* sp. prefers cyanobacteria over green algae (Zhang et al., 2018), but population losses from grazing only outpace cyanobacterial growth rates under low nutrient concentrations (Wilken et al., 2014). In certain instances, adding mixotrophic algae like *Ochromonas* sp. has been proposed as a way to manage cyanobacterial blooms by enhancing grazing losses to the cyanobacterial population (Zhang et al., 2020). Cyanobacterial grazing is only documented for a few bacteria taxa (Sun et al., 2018). Some level of direct cell-cell predatory activity has been reported in nutrient-rich co-cultures of *Fibrella aestuarina* (Baceroidetes) and *Nostoc muscorum* (Svercel et al., 2011). Endo- and epibiotic predation of different *Bdellovibrio* species have also been observed as well as group-hunting as reported for *Mixococcus* (Deltaproteobacteria) on filamentous and colonial cyanobacteria (Bauer and Forchhammer, 2021).

Ciliates are protozooplankton capable of grazing microbes and phytoplankton, including cyanobacteria (Kosiba and Krztoń, 2022). Several studies have shown that ciliates and rotifers, relatively small sized grazers, can individually or in combination graze cyanobacterial blooms enough to create net loss of cells within the cyanobacterial population. For example, Pajdak-Stós et al. (2020) showed that rotifers could break apart benthic mats of epiphytic filamentous cyanobacteria taxa, allowing ciliates and rotifers to remove cells from the mat via grazing. In planktonic settings the reverse may occur, with ciliates being able to initially graze and break apart aggregated cyanobacterial

biomass, followed by rotifers and ciliates being able to graze cyanobacterial cells faster than growth, in turn causing net loss and cyanobacterial bloom disappearance (Sweeney et al., 2022). These food web dynamics and grazing preferences by ciliate consumers, however, may vary with the nutritional quantity of the phytoplankton community. Deng et al. (2020) showed that similar to copepod food preference (see section 3.3.1), ciliates prefer high quality food sources (low C:N source) like eukaryotic algae over low nutritional value of cyanobacteria (high C:N source), and in turn may help cyanobacteria outcompete algal competitors via grazing on eukaryotic phytoplankton. Yet, although studies have shown short-term (days) reduction in ciliate growth rate by microcystin-producing cyanobacteria, ciliates seem relatively resilient to cyanobacterial toxins and have been shown remove or degrade microcystin in lab-based experiments (Combes et al., 2013; Kosiba et al., 2019).

Amoeba are phagotrophic protists that are substrate-bound interception feeders, and known cyanobacteria grazers. Amoebas employ "selective digestion"; prey selection and discrimination does not occur prior to ingestion, although cyanobacteria prey taste and toxicity does impact protist feeding as amoebae actively select nutritive food particles, and excrete toxic or unpalatable prey (Xinyao et al., 2006). In lab grazing experiments, filamentous cyanobacteria (e.g., *Dolichosperumum* (formerly *Anabaena*), *Raphidiopsis* (formerly *Cylindrospermum*), *Gloeotrichia*, and *Phormidium* sp.) were consumed by amoebas at clearance rates of 0.332 to 0.513 nL amoeba^{-1} h^{-1} (Xinyao et al., 2006). Grazing was size-selective, as some cyanobacteria (e.g., *Aphanizomenon flos-aquae, Oscilltoria tenuis,* and *Calothrix* sp.) exceeded the size threshold (Laybourn-Parry et al., 1987; Xinyao et al., 2006). Additionally, amoebas only ingested the vegetative cells, leaving the akinetes and heterocysts intact (Xinyao et al., 2006).

3.4. Resting Cells and Programmed Cell Death (PCD)

Resting stage cells and programmed cell death (PCD) are defined cyanobacterial population loss processes because they remove cells from the water column (Fig. 1J). As discussed below, however, resting cells and endogenous loss processes have been shown to be spurred by decreases in growth limiting factors (nutrients, temperature, light; Box 1; Lewis and Roberson, 2022). Thus, although growth and loss are separated mathematically by process modeling equations (Box 1), growth limitation can help accelerate resting cell production and PCD loss processes. Below we show relevant examples from the literature, but see Aguilera et al. (2021) and Franklin (2021) for more in-depth reviews on endogenous loss processes on cyanobacterial populations.

Resting stage cells, also known as akinetes, are a survival mechanism adapted by some cyanobacterial taxa. These specialized cells differentiate from vegetative cells to form a thick cell wall capable of withstanding a wide range of adverse conditions (i.e., drying, low temperatures, low light). Vegetative cells have been shown to differentiate into akinetes as a response to various environmental conditions and resource limitations (Adams and Duggan, 1999), such as nutrients (Meeks et al., 2002), light intensity and quality, temperature changes (Kaplan-Levy et al., 2010), and ion concentrations (Sukenik et al., 2007). Some studies show that akinetes form when blooms reach the stationary phase of growth (Meeks et al., 2002), resulting in a direct loss of part of the vegetative biomass (e.g., ca. 10 % in the case of *C. raciborskii* and *A. gracile*) through differentiation and subsequent sedimentation (Mehnert et al., 2014). Olli et al., (2005) evaluated the effects of nutrient additions on akinete differentiation in two populations of cyanobacteria (*Dolichospermum lemmermanni* and *Anabaena cylindrica*). Additions of nutrients significantly impacted akinete production for *A. lemmermannii*, where akinete production was highest when no P was added. In contrast, when P was added, this species allocated more resources toward vegetative cell growth. This pattern was not observed for *A. cylindrica*, and light and temperature did not impact akinete production for either species in Mehnert et al. (2014).

Furthermore, the authors noted that akinete differentiation and sedimentation can play an important role in actively growing blooms by alterations in resource allocations for growth vs. survival. Akinete differentiation results in less vegetative cells being developed, and hence less resources being used to sustain or increase cyanobacterial populations.

Programmed cell death (also known as regulated cell death) refers to non-accidental cell death in response to various internal or environmental triggers (Fig. 1J; Aguilera et al., 2021). PCD in cyanobacteria has been studied mostly in cultures, often triggered by atypical conditions such as high salinity and the presence of herbicides and oxidants (see summary in Aguilera et al., 2021). Nevertheless, an increasing body of evidence is showing that PCD plays an important role in controlling cyanobacterial populations under natural conditions. This was shown for bloom forming freshwater species such as *Microcystis* (Hu and Rzymski, 2019; Sigee et al., 2007), marine species such as *Trichodesmium* (Berman-Frank et al., 2004; Spungin et al., 2018), as well as globally significant picocyanobacterial taxa such as *Synechococcus* and *Prochlorococcus* (Llabrés et al., 2011). PCD, although tightly coupled with community-wide survival mechanisms under stressful conditions (Barteneva et al., 2022 and references therein), can lead to significant losses of cyanobacterial cells from a population (Bar-Zeev et al., 2013; Spungin et al., 2018). While PCD is an established loss process in cyanobacterial populations, and has been shown to be significant in the decline of eukaryotic phytoplankton (e.g., Choi et al., 2017 and references therein), evidence on the magnitude of the PCD effect on cyanobacterial bloom demise in natural systems is still scarce.

4. Bloom Management Strategies

Many of the loss processes presented above have been successfully used in management applications to reduce cells in the standing stock of cyanobacterial bloom populations. Methods for cyanobacterial biomass removal can be divided into physical, chemical, and biological treatments (Gallardo-Rodríguez et al., 2019; Kibuye et al., 2021; Li et al., 2022).

4.1. Physical treatments

Physical methods include aeration, mixing, inflow and outflow manipulation, and surface skimming. In general, the size and the morphology of the system as well as the infrastructure required to maintain the treatment greatly impacts the efficacy of physical approaches. For some methods, such as sonication, the evidence-base is lacking and not thus not discussed further (Lürling et al., 2016). The effectiveness of other methods have not been tested scientifically (e.g., shading and surface skimming), but can be modeled relatively easily. Below, we explain in more detail some well-studied physical methods, such as aeration, flushing, and mixing.

Visser et al. (2016) reviewed several studies where artificial mixing was used to combat cyanobacterial blooms and found that artificial mixing of relatively deep lakes can be an effective bloom management strategy, but in non-stratifying waters, artificial mixing can be counterproductive, as enhanced sediment P release fuels cyanobacterial blooms (Blottière et al., 2014; Lürling et al., 2016). In short, artificial mixing in stratifying waters allows non-buoyant taxa to remain suspended, increasing competition with cyanobacterial species, as well as causing the existing cyanobacterial species to be entrained, limiting access to nutrients; both processes seem to help cells active PCD/resting cells (i.e., sedimentation out of the water column). For example, artificial mixing was applied in Lake Nieuwe Meer, Netherlands, resulting in decreased sedimentation for diatoms and chlorophytes and subsequently, increased resource competition for *Microcystis* (Huisman et al., 2004; Visser et al., 1996). Artificial mixing in non-stratifying aquatic systems like shallow lakes or ponds, however, is counterproductive in cyanobacterial bloom management as artificial mixing in these systems

(<12 m) leads to enhanced sediment resuspension (Blottière et al., 2014; Lürling et al., 2016), in turn causing P release from the sediment that fuels blooms (Zhan et al., 2022). Additionally, cyanobacterial taxa like *Raphidiopsis* sp. may be adapted to relatively low light conditions, and thus can withstand being mixed in aphotic or relatively low light conditions during artificial mixing (Antenucci et al., 2005). Moreover, there has been little evidence that artificial mixing can be effective at bloom management in large lakes (Paerl and Otten, 2013a). Flushing has also been considered for bloom management. Given that the population growth rate of large bloom forming cyanobacteria can be lower than that of eukaryotic competitors, lake managers have tried reducing lake residence time through increased flushing to remove blooms, or selective flushing of specific areas of the water column to flush cells from the system (i.e., surface releases to flush buoyant cyanobacterial cells). The feasibility to control *Microcystis* blooms in the Dutch Lake Volkerak by reducing residence time under the critical limit for population maintenance was studied by Verspagen et al. (2006). Flushing has helped successfully reduce blooms in some systems (e.g., Ford Lake, Michigan), but water availability during droughts can hamper flushing efforts (Lehman, 2014).

4.2. Chemical treatments

Chemical approaches involve the addition of flocculants and coagulants (which are also used for P reduction), as well as the use of algaecides when a rapid reduction in cyanobacteria is required. Flocculant and coagulant addition is designed to remove cyanobacteria from the water column through the addition of a material that adheres to cyanobacterial cells before sinking to the lake bottom. Modified kaolinite clays are commonly used (Verspagen et al., 2006; Yu et al., 2017), but flocculation of cyanobacteria in the lab has also been achieved when chitosan has been used to modify cheap and inert materials like local soils (Noyma et al., 2016; Zou et al., 2006) and coal fly ash (Yuan et al., 2016). Flocculants have been shown to reduce cyanobacteria biomass throughout the water column in both the field and the lab for taxa such as *A. flos-aquae* (Waajen et al., 2016), *Microcystis* sp. (Noyma et al., 2016; Verspagen et al., 2006; Zou et al., 2006), and *Sphaerocavum brasiliense* (Noyma et al., 2016).

The most common algaecides for reducing cyanobacterial blooms are copper (Cu)-based. Copper sulfate, for example, has been used to control blooms for over a century (Moore and Kellerman, 1905). It is a cost-effective algaecide with a high efficacy, but it has been associated with high mortalities of both vertebrate and invertebrate species (Kibuye et al., 2021), and sometimes results in altered lake biogeochemistry (Song et al., 2011). Recently, hydrogen peroxide (H_2O_2), has emerged as an alternative algaecide for reducing cyanobacteria from lakes. Some studies have shown that cyanobacterial taxa are more sensitive to low concentrations of H_2O_2 than other phytoplankton and that H_2O_2 treatments may be a way to selectively reduce cyanobacteria (Drábková et al., 2007; Matthijs et al., 2012; Weenink et al., 2015). However, there remain many unknown long- and short-term effects of this strategy, including, for example, whether these low concentrations are effective on a wide range of cyanobacterial taxa, whether it stimulates the release of cyanotoxins through cell lysis (Piel et al., 2019), and whether there are unwanted or unexpected negative impacts on other components of the food web. Weenink et al. (2022) tested the sensitivity of a wide range of freshwater zooplankton and macro-invertebrates and found that sensitivity varied greatly between taxa, resulting in a potential trade-off between efficacy of controlling cyanobacteria and harming the most sensitive animals like the rotifer *Brachionus calyciflores* and key cyanobacterial-grazing cladocerans like *Ceriodaphnia dubia* and *Daphnia pulex* through the treatment.

4.3. Biological treatments

Biological treatments can be defined as an intervention that takes

place in parts of the aquatic food webs (Stroom and Kardinaal, 2016). Examples of biological treatments include the use of allelopathic macrophytes, which compete with the cyanobacteria for resources and emit cyanobacteriocidal compounds, and organism-based top-down control using predators, pathogenic bacteria, and viruses (Gallardo-Rodríguez et al., 2019; Li et al., 2022 and references therein). The use of top-down trophic cascades (i.e., biomanipulation; *sensu* Shapiro, 1975) to increase herbivorous zooplankton biomass to reduce cyanobacterial biomass via direct consumption of bloom forming phytoplankton was proposed decades ago (Jeppesen et al., 1990; Shapiro, 1975). Biomanipulation resulting in enhanced grazing pressure on cyanobacteria has resulted in successful applications to control blooms, at least in northern temperate systems where *Daphnia* dominate the zooplankton community (reviewed in Triest et al., 2016). Increased zooplankton, however, does not always reduce bloom forming cyanobacteria because consumption depends on defensive traits of the cyanobacteria (e.g., morphology, toxin production) as well as herbivore traits (e.g., grazing mode, tolerance, prey size spectrum; see section 3.3). Increasing benthic filter feeding bivalves have been suggested as well, and at times applied successfully, as a means of top-down control of bloom forming cyanobacteria, although again, the traits of both cyanobacteria and bivalves are key regulators of top-down control (Dionisio Pires et al., 2007, 2005; Sun et al., 2022). Thus, while top-down grazing can be a loss process for cyanobacteria, herbivore traits may constrain grazing to eukaryotic taxa, which in turn can help favor cyanobacteria dominance (Leitão et al., 2018).

4.4. Considerations for bloom treatment selection

There are numerous factors that affect the cyanobacterial bloom reduction strategy that managers select: physicochemical properties of the water body to be treated (e.g., pH, alkalinity, nutrient concentrations, depth, and area), the cyanobacterial species to be removed (e.g., unicellular *vs.* filamentous; toxic *vs.* non-toxic), bloom density, urgency of treatment, and costs (Mackay et al., 2014). Zeng et al. (2023) compared the efficiency, duration, and costs of different approaches to remove algal blooms and found that similar methods may have an efficiency difference of 30 %, but different approaches to reduce blooms can independently or combined reach up to 100 % removal of the bloom biomass. However, an important consideration for choosing a treatment approach is the impact on the ecosystem. For example, chemical agents such as algaecides may have relatively long residence times in the water and thus may also act on non-target organisms other than the bloom (Brêda-Alves et al., 2021). They may also lead to cell lysis, which is not ideal to because lysed cells release dissolved cyanotoxins into the water, subsequently affecting the entire ecosystem (Kenefick et al., 1993; Zhou et al., 2013). In addition, the carbon footprint of some of the treatments should be considered, as the energy demand of manufacturing, operation, and transportation might be relatively high, for instance the application of lanthanum-based bentonite coagulants or artificial mixing. Finally, when considering and implementing any type of control measure it is critical to include ecological understanding of the cyanobacteria in the engineering design. Typically, the failures of treatment measures, such as artificial mixing, can be attributed to the lack of key knowledge of cyanobacterial traits (see Mantzouki et al., 2016; Visser et al., 1996) and application in systems that are ill-fitted for the treatments (Lürling et al., 2016).

5. Perspectives and challenges in predicting climate change effects on cyanobacterial population dynamics

Climate change has been shown to increase cyanobacterial population growth through increases in temperature, thermal stratification strength, nutrient loading, and changes in food web dynamics (Elser, 1999; Song et al., 2023; Zepernick et al., 2023); however, the effects of climate change on loss processes are less explored. Tropicalization - the

poleward shift of tropical species due to warming - should support an increased niche for cyanobacterial blooms via the direct effect of temperature increases on cyanobacterial growth rate (*sensu* Gobler et al., 2017; Paerl and Huisman, 2008). Although many studies have posited that temperature increases/tropicalization will cause increases in cyanobacterial blooms, empirical studies have shown mixed results with some finding increases (Ho et al., 2019) while others have not (Wilkinson et al., 2021). The lack of an increase in blooms may be due to increases in loss processes on cyanobacterial populations. For example, water temperature affects the survival rate of free cyanophages and their potential virulence, with a preference of high temperature up to 50°C (Grasso et al., 2022), indicating that infections (see section 3.2) may help offset increased growth of cyanobacterial populations due to temperature increases. Additionally, climate change may also alter food webs, which in turn may change the balance between growth and loss processes for cyanobacterial populations. For example, higher temperatures may increase fish planktivory, causing fewer large filter feeders like *Daphnia* and increases in copepods, causing less grazing on cyanobacterial taxa relative to eukaryotes and hence increases in cyanobacteria (Ger et al., 2016). These examples demonstrate the complexity in trying to predict how loss processes will affect cyanobacterial blooms in the face of climate change, especially when the relative importance and magnitude of loss processes in bloom dynamics under current conditions is not well understood or quantified. We advocate that the responses of loss processes under climate change should be given greater priority, considering their importance in determining the overall net effect of climate change impacts on cyanobacteria blooms, along with their implications for bloom management.

6. Conclusions

Cyanobacterial bloom dynamics are governed by the balance between growth and loss processes. Considerable attention has been given to the processes that drive or promote cyanobacterial population growth and limitations on growth, but cyanobacterial population loss processes are less studied (Box 1). In this review, we built on previous work by Reynolds (1984) and others by providing an in-depth synthesis of known loss processes as well as those that are applied in bloom management. While understanding the cause of blooms is crucial, we posit that understanding the processes that lead to the loss of biomass is equally important, especially in systems where blooms are established and occur regularly. Cyanobacterial traits such as buoyancy and resilience to oxidative stress (section 2), *in situ* physicochemical conditions like thermal structure (section 2) and nutrient/light resource (Section 4) dynamics, and the microbial, phytoplankton, and consumer community composition (section 3) affect how and when loss processes can override cyanobacterial bloom growth processes to make cyanobacterial blooms disappear. A deeper knowledge of the loss processes affecting cyanobacterial blooms will provide a more holistic understanding of bloom ecology, which can improve modeling, prediction, and management of blooms in the face of climate change.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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