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REVIEW

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Cyanobacterial blooms in oligotrophic lakes: Shifting the high-nutrient paradigm

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Abstract

1. Freshwater cyanobacterial blooms have become ubiquitous, posing major threats to ecological and public health.
2. Decades of research have focused on understanding drivers of these blooms with a primary focus on eutrophic systems; however, cyanobacterial blooms also occur in oligotrophic systems, but have received far less attention, resulting in a gap in our understanding of cyanobacterial blooms overall.
3. In this review, we explore evidence of cyanobacterial blooms in oligotrophic freshwater systems and provide explanations for those occurrences.
4. We show that through their unique physiological adaptations, cyanobacteria are able to thrive under a wide range of environmental conditions, including low-nutrient waterbodies.
5. We contend that to fully understand cyanobacterial blooms, and thereby mitigate and manage them, we must expand our inquiries to consider systems along the

trophic gradient, and not solely focus on eutrophic systems, thus shifting the *high-nutrient paradigm* to a *trophic-gradient paradigm*.

KEYWORDS
climate change, cyanobacterial blooms, HABs, nutrients, oligotrophic

1 | INTRODUCTION

Cyanobacterial blooms are a globally significant challenge in marine and freshwater systems. A central theme to this body of work is that blooms are caused by anthropogenic eutrophication (Dokulil & Teubner, 2000; Lürling et al., 2018). While there is a wealth of evidence that high nutrient loads promote cyanobacterial blooms, there is also widespread evidence that blooms occur in oligotrophic systems (Callieri et al., 2014; Carey, Ewing, et al., 2012; Carey et al., 2014; LeBlanc et al., 2008; Molot et al., 2021; Salmaso et al., 2015; Sterner et al., 2020; Winter et al., 2011), and that they are not a recent phenomenon (Ewing et al., 2020). Some metalimnetic bloom-forming cyanobacteria, such as *Planktothrix rubescens* in Lake Bourget France, Switzerland, even appeared in a context of strong re-oligotrophication because of increased light availability in the metalimnion (Jacquet et al., 2005). Moreover, despite a worldwide trend towards eutrophication, there is a substantial number of lakes where successful restoration programmes have reduced nutrient levels to mesotrophic or oligotrophic conditions, yet blooms persist (Pomati et al., 2012).

There are a number of reviews that describe the many adaptations of cyanobacteria that allow them to thrive under a wide range of environmental conditions, including low nutrient concentrations (e.g. Carey, Ibelings, et al., 2012). Despite this evidence, the high-nutrient paradigm has persisted, and the conditions driving blooms in low-nutrient systems are largely unexplored, resulting in a lack of understanding of these events. Identifying mechanisms that trigger and sustain blooms across trophic states is critical for a comprehensive understanding of global increases in cyanobacterial dominance. Overlooking cyanobacterial blooms in oligotrophic waters has resulted in an incomplete understanding of bloom ecology and, subsequently, ineffective mitigation efforts.

Cyanobacterial blooms have been defined in several ways, but here we define a freshwater pelagic cyanobacterial bloom as rapid growth or aggregation of cyanobacterial biomass in some or all of the water column, which may lead to the occurrence of surface scums or metalimnetic chlorophyll maxima (following Smayda, 1997). The "oligotrophic" definition also lacks a consensus. Here, we define oligotrophic lake systems by Carlson's Trophic State Index (TSI), with total phosphorus (TP) ≤12 μg/L, chlorophyll *a* (chl-*a*) ≤2.6 μg/L, or Secchi depth >4 m (Carlson, 1977) during mid-summer in the epilimnion, given that blooms typically occur during mid- to late summer. We recognise, however, that categorising lakes by average state variables may not fully capture the variability of stochastic loading and mixing events, and that intermittent nutrient pulses may be important mediators of bloom formation. Further, chl-*a* and TP samples collected during a bloom event would most certainly put most lakes in the mesotrophic or eutrophic categories; therefore, we should rely on typical seasonal averages or baseline values for indices to classify the trophic state of lakes.

Here, we provide an assessment of the current understanding of oligotrophic cyanobacterial blooms and the abiotic and biotic factors that promote them. Our review suggests that while nutrients contribute to bloom formation and maintenance, there are several mechanisms that allow cyanobacteria to dominate across trophic states, including oligotrophic systems. We provide further insight into how these mechanisms are expected to interact under future climate conditions to promote and sustain cyanobacterial blooms in oligotrophic ecosystems.

2 | DOCUMENTED BLOOMS IN OLIGOTROPHIC LAKES

The documentation of cyanobacterial blooms in oligotrophic lakes is relatively limited compared to those in nutrient-rich lakes; however, evidence of blooms in oligotrophic lakes does exist. In addition to documented blooms, there is evidence that cyanobacteria are also increasing in relative abundance in oligotrophic systems. Freeman et al. (2020) identified 28 nutrient-poor Swedish lakes in which the relative abundance of cyanobacteria increased in 21% of the lakes that were sampled between 1998 and 2013. Genera that were present in the subset of lakes that experienced increases included *Chroococcus*, Dolichospermum (formerly *Anabaena*), and *Merismopedia*. Similarly, Winter et al. (2011) noted cyanobacteria were increasing in low-nutrient Ontario shield lakes sampled from 1994 to 2009. The primary genera observed in those lakes were *Aphanizomenon*, *Dolichospermum*, *Microcystis*, and *Gloeotrichia*. Sorichetti et al. (2014b) evaluated 25 oligotrophic lakes located in Ontario, Canada and found that the dominating species were *Microcystis*, *Dolichospermum*, and *Aphanizomenon*, and that the highest relative abundances of cyanobacteria occurred in lakes with the lowest chl-*a* and TP concentrations and phytoplankton abundances.

We compiled a list of oligotrophic lakes with reports of cyanobacterial blooms (Figure 1 and Table S1) and found that these lakes are geographically widespread with a wide range of lake morphometries. However, many blooms are not documented in peer-reviewed journals and reports and are only discoverable through direct connections to water resource managers. Further, some peer-reviewed journal articles that note blooms in oligotrophic lakes do not

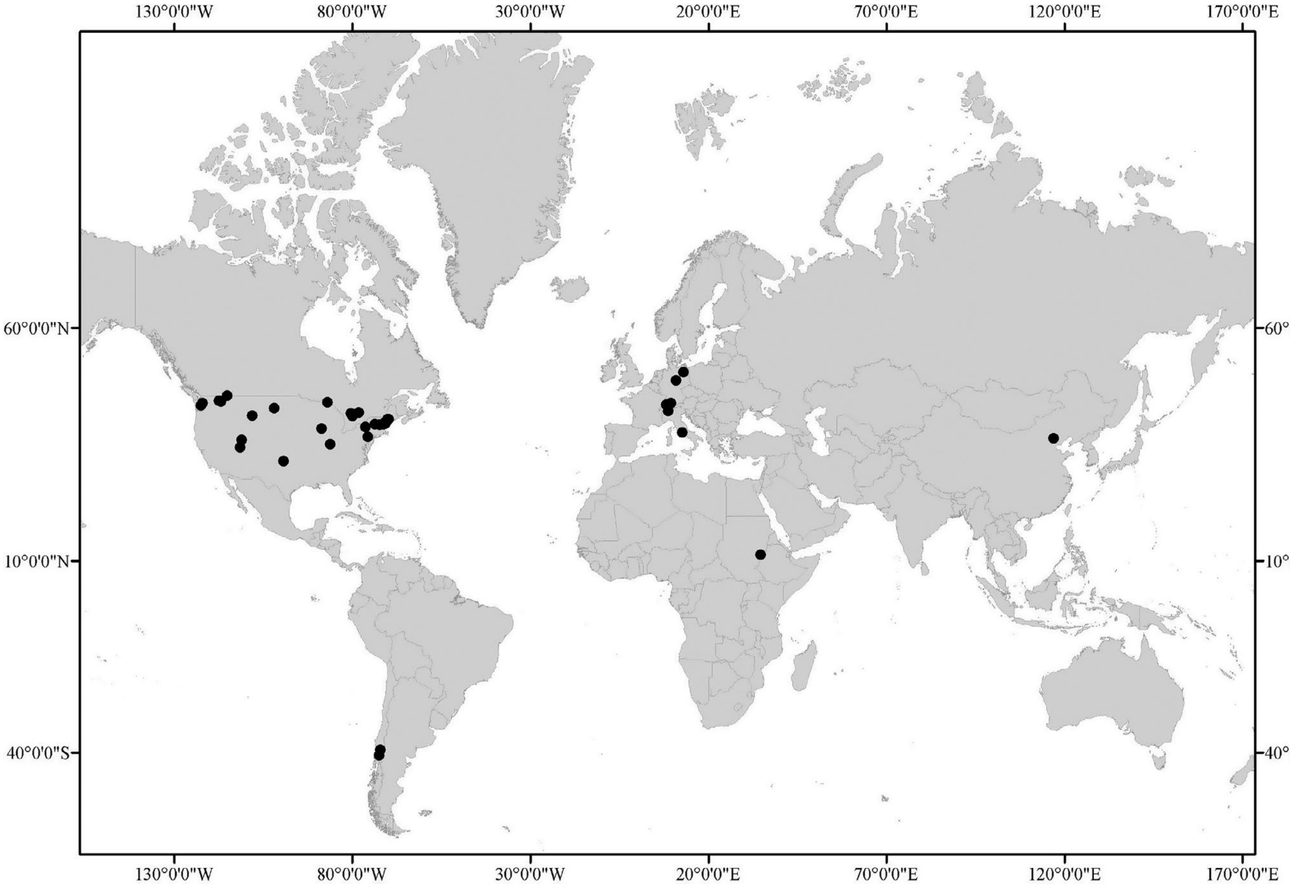

FIGURE 1 Map of locations for cyanobacterial blooms in oligotrophic systems reported in Table S1. Lakes are located in North America, South America, Africa, Asia, and Europe. World map shapefile provided from https://thematicmapping.org/downloads/world_borders.php

provide information for individual lakes (e.g. Sorichetti et al., 2014a, b). We found that ~12 genera of cyanobacteria from the orders Chroococcales, Nostocales, Oscillatoriales, and Synechococcales tend to dominate the phytoplankton community during the blooms and belong to a variety of Morpho Functional Groups (MFGs, sensu Salmaso & Padisák, 2007), highlighting the diverse traits that help cyanobacteria to outcompete eukaryotic algae in oligotrophic systems (Table 1).

3 | CYANOBACTERIAL TRAITS FAVORING DOMINANCE IN LOW-NUTRIENT SYSTEMS

3.1 | Dormancy and specialised cells

Many cyanobacteria taxa can remain dormant under unfavourable environmental conditions. Strategies for dormancy vary across genera, ranging from slowed metabolism in a vegetative state (Verspagen et al., 2005) to differentiation into spore-like cells produced by certain filamentous cyanobacteria called akinetes that arise from vegetative cells (Wildon & Mercer, 1963). Larger than vegetative cells and encased in thick glycolipid and polysaccharide-rich cell walls, akinetes allow some cyanobacteria to suspend metabolism and sink to the sediment for dormancy, typically under unfavourable environmental conditions such as low temperature, desiccation, or phosphate (PO_4^{3-}) limitation, with germination occurring when more favourable conditions resume (Kaplan-Levy et al., 2010; Reynolds, 2006). Phosphate limitation has been identified as a trigger of akinete differentiation in oligotrophic systems (Callieri et al., 2014; Kaplan-Levy et al., 2010). Akinetes, an important intermediate phase between previous and future blooms, enable recurrent cyanobacterial blooms through the recruitment of heterocystous taxa from the sediment (Carey et al., 2008), especially in shallow embayments of oligotrophic lakes (Cottingham et al., 2021).

For blooms to arise from dormant akinetes, conditions favourable for germination and recruitment must occur, which are not yet fully understood and vary among systems. Increased light, temperature, nutrient enrichment, and sediment resuspension are all potential factors influencing germination (Barbiero & Welch, 1992; Kaplan-Levy et al., 2010). Callieri et al. (2014) identified fluctuations in lake levels and subsequent phosphorus (P) release from littoral sediments as responsible for the germination of *Dolichospermum lemmermannii* akinetes and the blooms that followed. Carey et al. (2008) also found that P additions positively influenced *Gloeotrichia echinulata* akinete germination in an oligotrophic lake, demonstrating the adaptive value of the akinetes for a cyanobacterial population to re-establish after P-limitation. While a thick outer envelope over the cell wall enables akinetes to withstand environmental stresses, this envelope

TABLE 1 Summary of cyanobacteria genera, traits, and Morpho Functional Groups (MFGs)[a] for documented blooms in oligotrophic systems in Table S1

Taxa	Traits summary	MFG (from Salmaso & Padisák, 2007)
Aphanizomenon gracile	Thick filaments, produce akinetes, can regulate buoyancy	Nostocales (5e)
Aphanocapsa sp.	Large non-vacuolated colonies, large surface area:volume allows slower sinking from surface	OtherChroo (5c)
Aphanothece sp.	Large non-vacuolated colonies, large surface area:volume allows slower sinking from surface	OtherChroo (5c)
Chroococcus limneticus	Large non-vacuolated colonies, large surface area:volume allows slower sinking from surface	OtherChroo (5c)
Dolichospermum sp. (formerly *Anabaena* sp.)	Thick filaments, produce akinetes, can regulate buoyancy	Nostocales (5e)
Gloeotrichia echinulata	Thick filaments, forms large colonies, produce akinetes, can regulate buoyancy	Nostocales (5e)
Microcystis sp.	Large vacuolated colonies, can regulate buoyancy, large surface area:volume allows slower sinking from surface, over-wintering dormant cells	LargeVacC (5b)
Planktothrix agardhii	Thin filaments, can regulate buoyancy, over-wintering dormant cells	FilaCyano (5a)
Rivularia sp.	Thick filaments, large surface area: volume allows slower sinking from surface	Nostocales (5e)
Synechococcus sp.	Large non-vacuolated colonies, large surface area:volume allows slower sinking from surface	OtherChroo (5c)
Synechocystis sp.	Small non-vacuolated colonies, large surface area:volume allows slower sinking from surface	SmallChroo (5d)
Woronichinia sp.	Large vacuolated colonies, can regulate buoyancy, large surface area:volume allows slower sinking from surface	LargeVacC (5b)

[a] Cyanobacterial MFGs presented in this table represent 1 of 11 MFG categories that include all phytoplankton as per Salmaso and Padisák (2007). Cyanobacteria have two MFGs within the MFG framework: MFG 4 for unicellular cyanobacteria and MFG 5 for cyanobacteria that can form colonies. Observed blooms of cyanobacteria in oligotrophic systems were all within MFG 5, indicating colony formation is an important trait for bloom formation.

either develops a pore or dissolves altogether before germination (Miller & Lang, 1968). Further, akinetes maintain a low level of respiration, indicating that some materials must be able to pass through the cell wall (Fogg et al., 1973). Light has also been identified as an important factor in germination, but its relative importance varies both among species and systems (Barbiero & Welch, 1992; Kaplan-Levy et al., 2010). Oligotrophic systems have deeper light penetration than mesotrophic and eutrophic systems (Carlson, 1977), which may increase the area and intensity of light exposure at the sediment surface, resulting in a higher akinete germination rate than in eutrophic systems.

3.2 | Buoyancy regulation

Lake surface water temperatures are increasing globally, resulting in longer and more stable periods of stratification (Woolway & Merchant, 2019), providing an advantage to cyanobacteria that can regulate their buoyancy and remain in the illuminated surface mixed layer (Reynolds, 2006). Buoyancy is mediated by gas-vesicles, which are hollow protein structures filled with air that have evolved to withstand both turgor and hydrostatic pressure (Walsby, 1994). Storage of dense carbohydrates from photosynthesis decreases buoyancy, resulting in diel cycles of sinking and floating as cells lose buoyancy during daylight through photosynthesis and regain buoyancy in the dark through respiration (Ibelings et al., 1991). Under prolonged periods of low light, cyanobacteria upregulate the expression of genes that encode for gas-vesicle proteins, enhancing their buoyancy (Walsby et al., 1991). Walsby et al. (1991) examined the buoyancy of *Dolichospermum. lemmermannii* blooms in Lake Windermere (U.K.) and found that *D. lemmermannii* stimulated the production of new gas-vesicles during a period of deep mixing. When mixing subsided and filaments floated up, cells were unable to produce sufficient ballast to overcome buoyancy, resulting in persistent surface water blooms. Further, *D. lemmermannii* possessed stronger gas vesicles than other species of the same genus, allowing the cyanobacteria to descend deeper in the water column without collapse, providing better access to hypolimnetic nutrients, which could provide an important advantage in nutrient-poor surface waters of oligotrophic lakes.

In the absence of mixing, buoyant cyanobacteria float upwards, forming surface blooms. These can accumulate on the shore, forming scums, even in oligotrophic lakes with low overall cyanobacterial biomass (Carey, Ibelings, et al., 2012; Sterner et al., 2020). Surface bloom formation may enhance access to carbon dioxide (CO_2) from the atmosphere (Paerl & Ustach, 1982; Visser et al., 2016); however, complete inorganic carbon (C) depletion in scums can still occur, caused by the high biomass and local C demand (Ibelings & Maberly, 1998). Other advantages of buoyancy control include better access to nutrients by descending into the relatively nutrient-rich hypolimnion (Cottingham et al., 2015, but see Bormans et al., 1999), and the ability to remain in the warmer water of the epilimnion. Thus, buoyancy may allow cyanobacteria in oligotrophic systems enhanced access to nutrients and favourable temperatures and light throughout the water column, and is probably why there are well-documented blooms of cyanobacterial genera that can regulate buoyancy in multiple oligotrophic lakes in North America, South America, Europe, Africa, and Asia (Figure 1 and Table S1).

In addition to epilimnetic blooms, buoyancy regulation is essential for the formation of deep chlorophyll maxima of species such as *Planktothrix rubescens*, *Cyanobium* sp., and *Aphanizomenon flos-aquae* in the metalimnion of deep, oligo-mesotrophic lakes (Selmeczy et al., 2016). Having a filamentous morphology and maintaining near-neutral buoyancy, these cyanobacteria oscillate around their position in the metalimnion, where they thrive on having access to both light—through efficient light harvesting mechanisms—and nutrients in the hypolimnion (Walsby & Schanz, 2002).

3.3 | Nutrient uptake

The evolution of cyanobacteria in low-nutrient systems (Bjerrum & Canfield, 2002) has provided them with the ability to efficiently take up and store nutrients in various forms (Cottingham et al., 2015). They can store both excess P (as polyphosphates) as well as excess nitrogen (N; as cyanophycin), allowing them to sustain populations under nutrient-deprived conditions (Kromkamp, 1987). Cyanobacteria have a relatively high PO_4^{3-} uptake affinity compared to eukaryotic taxa, enabling them to sustain high growth rates under P-limitation (Dignum et al., 2005). Many cyanobacteria also have either internal or external (via their microbiome) phosphatases, allowing them to utilise organic P in addition to inorganic forms (Carey, Ibelings, et al., 2012). Whitton et al. (1991) evaluated the role of phosphatases in P uptake and storage in 50 cyanobacteria strains using six different sources of organic P and one inorganic P source. In the absence of a P source, 10 strains (including one *Dolichospermum*) were able to grow for several days, demonstrating their ability to store P. Despite species-specific variability in the ability to use sources of organic P, Whitton et al. (1991) demonstrate that some cyanobacteria can access a P pool less available to other phytoplankton taxa, providing an advantage under P-limited conditions.

De Nobel et al. (1997) evaluated competition for P between two N-fixing cyanobacteria, *Dolichospermum* and *Aphanizomenon*. During N-fixation and under P-limited conditions, *Dolichospermum* outcompeted *Aphanizomenon* through adjustments in its maximal growth rate and greater P uptake. The ability to fix atmospheric N_2 provides cyanobacteria with a pool of N not available to eukaryotic algae, thus providing a substantial resource advantage. N-fixation can support up to 91% of the N demand for an oligotrophic bloom and as much as 81% of a lake's annual N inputs (e.g. *Nodularia* sp. blooms in oligotrophic Pyramid Lake, NV, U.S.A.; Horne & Galat, 1985). Although several species of cyanobacteria can fix N_2, P and iron (Fe) limitation can constrain N_2-fixation because Fe is a cofactor in the nitrogenase enzyme complex (Mills et al., 2004), and due to the high energy requirement of N_2-fixation, low light conditions may make this pathway for nutrient uptake less desirable.

Access to reduced Fe may promote cyanobacterial dominance in oligotrophic systems (Molot et al., 2014; Sorichetti et al., 2014a, b; Verschoor et al., 2017). Fe is made bioavailable geochemically through internal loading from anoxic eutrophic sediments, catchment runoff, or aeolian dust. While anoxia drives the release of Fe--PO_4^{3-} bound in the sediment by modification of the redox potential, cyanobacteria can also mediate this process under oxic conditions via siderophore production and scavenging of bound Fe (Wilhelm & Trick, 1994), alleviating Fe limitation. Eichner et al. (2020) showed plausible molecular evidence that colonies of *Trichodesmium* (marine cyanobacterium) can mediate Fe leaching. Fe leaching is a fundamental bacterial process for decoupling PO_4^{3-} from Fe (Smolders et al., 2006), and may provide cyanobacteria with an increased benefit when competing with eukaryotes in oligotrophic systems.

Nutrient contributions from the food web via recycling from grazers and consumers may also be important for blooms in oligotrophic systems, which is highly relevant in determining phytoplankton dynamics in oligotrophic systems (Domaizon et al., 2003; Gutiérrez-Rodríguez et al., 2011; Jackson, 1980; Jiang et al., 2021; Livanou et al., 2019; Teira et al., 2019). Jackson (1980) found that zooplankton abundance and their filtration rate were unable to exceed phytoplankton growth rates. Further, an experimental study (Carrillo et al., 1995) showed that in a low-nutrient environment, nutrient release from higher trophic levels can be better utilised by cyanobacteria (*Cyanarcus* sp.) than other species of phytoplankton (*Chromulina nevadensis* and *Amphidinium* sp.), resulting in dominance in oligotrophic systems. The top-down or bottom-up control effects on cyanobacterial dynamics should be given more attention in oligotrophic bloom formation (Billen et al., 1990), especially under climate change pressures where grazers can respond at different rates than phytoplankton (Velthuis et al., 2017).

3.4 | Light

Cyanobacteria are well adapted to thrive under a wide range of light conditions (Dokulil & Teubner, 2000). Exoplasmic phycobilisomes, a component of the cyanobacterial photosynthetic apparatus (Reuter & Müller, 1993), probably play a role in this adaptation. These antennae are capable of absorbing light wavelengths in the green to orange part of the light spectrum (phycoerythrin and phycocyanin, respectively) that cannot be used by the chlorophyll–protein light harvesting complexes of most eukaryotic algae (Kirk 1994). In addition to efficient absorption in the visible light spectrum, cyanobacteria have a protein structure that allows them to use light in the far-red spectrum, giving them a further advantage for growth under severe light extinction (Kirk 1994). The capacity to effectively adapt to low irradiance at depth (often far <1% of incident light; Hamre et al., 2018) demonstrates that cyanobacteria are well adapted to not only the low light conditions of eutrophic lakes, but also the deep chlorophyll maxima that are often present in meso- and oligotrophic lakes (e.g. *Planktothrix rubescens*, *Cyanobium* sp., and *Aphanizomenon flos-aquae*; Scofield et al., 2017, Reinl et al. 2020).

At times of high solar irradiance, cyanobacteria are well equipped to handle high visible and ultraviolet (UV) conditions via photoprotective accessory pigments, extracellular polysaccharides produced by colonies and filaments (Ehling-Schulz & Scherer, 1999), and the production of UV-absorbing compounds (Carreto & Carignan, 2011). High irradiance results in a decrease in the size and number of phycobilisomes compared to low light conditions (Reuter & Müller, 1993), but the degree of photoacclimation of cyanobacteria varies among species. In eight *Dolichospermum* strains, a wide range of irradiance for optimal growth was observed, with the lowest being 80 μmol m^{-2} s^{-1} for *D. mendotae* and the highest being 360 μmol m^{-2} s^{-1} for *D. circinalis* (Zapomělová et al., 2010). Cyanobacteria also demonstrate chromatic adaptations, meaning that they are able to change their pigment composition in response to ambient light colours, and fill wavelength gaps using accessory pigments and phycobilisomes to capture light that can then be used to excite chl-*a* (Duxbury et al., 2009). These changes in pigmentation occur alongside adjustments in RuBisCO and light-saturated photosynthetic rates to achieve efficient light harvesting under low light conditions and efficient C assimilation under high irradiance (Dubinsky & Stambler, 2009). Moreover, buoyancy regulation enables cyanobacteria to migrate downwards and limit their exposure to visible and UV light when photo-inhibited (Deacon & Walsby, 1990; Ibelings & Maberly, 1998). The combination of buoyancy traits and adaptations to a wide range of light conditions give cyanobacteria enhanced flexibility to deal with changes in light amount and wavelength type relative to their eukaryotic counterparts.

3.5 | Carbon concentrating mechanisms

Many phytoplankton species can actively take up inorganic C from the water column, but the cyanobacterial carbon concentrating mechanism (CCM) is among the most efficient (Price et al., 2008). Cyanobacteria have evolved five different uptake pathways for CO_2 and bicarbonate (HCO_3^-), providing a competitive advantage over phytoplankton not using CCMs (Raven et al., 2008; Shapiro, 1997). In contrast to eukaryotic algae, cyanobacteria store RuBisCO in carboxysomes, so that the activation of cyanobacterial CCMs allows for the concentration of inorganic C near RuBisCO (Price et al., 2008). This decreases leakage and facilitates the conversion of HCO_3^- to CO_2 via carbonic anhydrase, resulting in efficient C-fixation (Price et al., 2008) relative to phytoplankton taxa not utilising CCMs. In eutrophic lakes, this mechanism is triggered in cyanobacteria when water column pCO_2 falls below atmospheric equilibrium (Morales-Williams et al., 2017), and could occur in oligotrophic surface blooms where high production depletes available inorganic C (Ibelings & Maberly, 1998). While CCM inorganic C transport systems are less diverse in oligotrophic systems, laboratory studies suggest that a greater diversity of transporters have been acquired through horizontal gene transfer as cyanobacteria have transitioned from the oligotrophic ocean to coastal and freshwater ecosystems (Rae et al., 2011). Variation in low and high affinity inorganic C uptake systems in *Microcystis* spp. may provide them with an advantage to adapt to future changes in C availability in the aquatic environment (Sandrini et al., 2014).

Plasticity in cyanobacterial CCM regulation reflects the evolution of CCMs over geological timescales in response to the variability in atmospheric CO_2 and oxygen (O_2) over several billion years (Van de Waal et al., 2019). The importance of active inorganic C uptake by freshwater cyanobacteria in oligotrophic lakes should depend on the availability of CO_2 and the relative proportions of available ambient CO_2 and HCO_3^-. These conditions vary with buffering capacity, influenced by lake morphometry, sediment, bedrock composition, and catchment inputs. In marine systems, including the high nitrate, low chl-*a* regions of the Southern Ocean analogous to large oligotrophic freshwater lakes, HCO_3^- is the dominant inorganic C species and phytoplankton communities rely primarily on CCMs for C-fixation (Cassar et al., 2004). Under elevated CO_2 conditions, dominant cyanobacteria strains are predicted to shift to those utilising bicA Ci transporter genes, which have a low affinity for HCO_3^- but facilitate high fluxes (Sandrini et al., 2016), demonstrating plasticity across a wide range of inorganic C conditions. Under experimental low dissolved inorganic C conditions, CCM utilisation has been shown to inhibit nutrient uptake in eukaryotic marine algae, demonstrating metabolic trade-offs between C-fixation and nutrient uptake (Huertas et al., 2000). Lakes in northern latitudes are also experiencing an increase in dissolved organic matter (DOM) inputs from the catchment, which is predicted to cause a community shift toward cyanobacteria in oligotrophic lakes due to their ability to access nutrients bound to DOM (Creed et al., 2018). Few studies have directly investigated cyanobacteria CCMs in oligotrophic lakes, although Vuorio et al. (2006) reported elevated $\delta^{13}C$ values for *Gloeotrichia echinulata* in Finnish lakes, which is consistent with the range of isotopic signatures for CCM utilisation in eutrophic lake phytoplankton (Morales-Williams et al., 2017). More work is needed to determine the importance of cyanobacterial CCMs in triggering and maintaining oligotrophic blooms.

4 | ABIOTIC CONDITIONS THAT PROMOTE CYANOBACTERIA IN OLIGOTROPHIC SYSTEMS

4.1 | Temperature

Cyanobacteria are well adapted to grow at a wide range of water temperatures. Although the mean optimal growth temperature for cyanobacteria and eukaryotic green algae is similar, approximately 29°C (Lürling et al., 2013), the positive slope of growth rate as a function of temperature is steeper for cyanobacteria (Visser et al., 2016). In a phytoplankton community consisting of cyanobacteria, diatoms, and green algae, De Senerpont Domis et al. (2007) demonstrated that cyanobacteria had higher growth rates relative to eukaryotic phytoplankton in experimental warming conditions. Kosten et al. (2012) also showed a strong correlation between cyanobacterial biomass and temperature, where overall algal biomass did not change significantly with temperature, but the relative abundance of cyanobacteria increased with warmer water temperatures. A positive relationship between cyanobacterial blooms and temperature, which may need further support, also appears to be self-propagating; intense light absorption by cyanobacteria's photosynthetic and photoprotective pigments can increase surface water temperatures within blooms relative to surrounding surface waters (Ibelings et al., 2003; Jones et al., 2005). Additionally, while lakes across the trophic gradient are warming as a result of anthropogenic climate change, oligotrophic lakes may be more sensitive to biogeochemical changes than eutrophic lakes. A modelling study of a eu- and oligotrophic lake demonstrated that oligotrophic lakes may have a lower threshold for nutrient cycling responses to temperature, particularly for N, but the precise reason for increased sensitivity is still an open question (Farrell et al., 2020).

Although correlations between blooms and warming surface waters, some cyanobacterial species can bloom under ice (Dokulil et al., 2014). For example, blooms of *Aphanizomenon flos-aquae* have been reported under the ice in oligo–mesotrophic lakes (Üveges et al., 2012), demonstrating that low temperatures do not prevent the proliferation of cyanobacteria. Cyanobacteria are commonly found under the ice and in other extreme environments, so it is not surprising that they may dominate in dark, cold, low-nutrient environments (Quesada & Vincent, 2012), although more work is needed to understand cyanobacterial physiology in these conditions.

4.2 | Upwelling events and wind mixing

By definition, macronutrients such as N and P limit phytoplankton growth in oligotrophic lakes. In some deeper stratified oligotrophic lakes, however, nutrient concentrations may be elevated in the hypolimnion during stratification (Cottingham et al., 2015). This is a result of reduced nutrient uptake below the thermocline due to light limitation and low temperatures, the physical density barrier to non-buoyant phytoplankton, nutrient accumulation from sediment release, and decomposition of plankton sinking losses from the epilimnion (Matzinger et al., 2007). These nutrients can enter the epilimnion during upwelling events caused by wind mixing or convective cooling (Crockford et al., 2015) and during seasonal overturn. Although a nutrient pulse driven by an upwelling event would be beneficial for eukaryotic algae as well as cyanobacteria, some cyanobacteria have higher uptake rates relative to their biomass (Litchman et al., 2016) as well as a greater storage capacity for nutrients (Kromkamp, 1987), which would allow them to outcompete their eukaryotic counterparts. This may be particularly true for oligotrophic systems where cyanobacteria with an ability for luxury uptake can sustain during poor nutrient conditions until an upwelling event occurs, replenishing the nutrients available in the epilimnion. Furthermore, due to the otherwise strong nutrient limitation during the growing season in the epilimnion, nutrient upwelling may be an important driver of bloom formation in oligotrophic lakes by bringing biomass from the meta- into the epilimnion. For example, in oligotrophic Lake Stechlin (Germany), mixing events can bring up a deep chlorophyll maximum (mainly *Dolichospermum* sp.) from the metalimnion to form surface blooms (Kasprzak et al., 2017).

In addition to the positive effect of mixing on nutrient availability, mixing can also stimulate cyanobacterial recruitment from the sediments to the water column, thereby further promoting blooms. Experimental work in laboratory mesocosms (Karlsson-Elfgren & Brunberg, 2004) as well as measurements of recruitment from oligotrophic Lake Sunapee (U.S.A.; Carey et al., 2014) showed that gentle mixing at the sediment-water interface can increase surface cyanobacterial densities. During 8 years of cyanobacterial recruitment monitoring at multiple sites in Lake Sunapee, Carey et al. (2014) observed that: higher *Gloeotrichia echinulata* recruitment was associated with greater lake mixing during late summer (as indicated by deeper thermoclines), lower Schmidt stability (a measure of the stratification strength), lower minimum air temperatures, and greater daily changes in water temperature.

5 | TRAJECTORIES OF FUTURE BLOOMS IN LOW-NUTRIENT SYSTEMS

5.1 | Increasing temperatures

Climate-induced changes in summer stratification and subsequent mixing regimes will be likely to increase hypolimnetic anoxia (Jane et al., 2021; Jenny et al., 2016) and rates of internal nutrient loading (North et al., 2014). In the stratified summer months, the epilimnion of deep oligotrophic lakes will probably become more nutrient deficient due to an earlier onset of stratification, with nutrients isolated in the hypolimnion for extended periods (Shimoda et al., 2011). With a shift from holomixis (full mixing once per year) to oligomixis (full mixing rarely), nutrients may be isolated from the epilimnion for multiple years (Mesman et al., 2021). Hence, although climate warming may lead to anoxia and enhanced release of nutrients from the sediment, nutrient availability in the productive upper zones of the lake may actually decrease and become available only in years with full overturn (see O'Reilly et al., 2003; Yankova et al., 2017). Because overturn is often characterised by low light and temperature conditions, not all cyanobacterial species would be equipped to thrive under these conditions, but several species have a wide range of adaptability to light conditions and temperatures (e.g. *Dolichospermum spp.* Dokulil & Teubner, 2000 and Zapomělová et al., 2010). This oligotrophication of the epilimnion of deep lakes could be advantageous for small cyanobacteria with efficient nutrient uptake and N-fixing capacity.

Winters without ice cover are also increasing in temperate regions, leading to a shift in mixing regime from dimictic to warm monomictic (Gerten & Adrian, 2002). Increasing reports of late-season (October–December) cyanobacterial blooms have been reported for lakes in Canada, including oligotrophic and mesotrophic lakes, and have been attributed to a delayed onset of ice cover and longer periods of stratification (Winter et al., 2011). A long-term study in a dimictic lake reported an increase in winter algal biomass during mild winters (Adrian et al., 1995). Following these mild winters, the maximum phytoplankton biomass occurred 1 month earlier and was dominated by cyanobacteria (Adrian et al., 1995, 1999). In Scandinavian lakes, cyanobacterial biomass has also increased in spring and early summer due to warmer winters (Weyhenmeyer, 2001). This may be particularly important for oligotrophic lakes, as many are found in higher latitudes with colder climates (Alin & Johnson, 2007) where loss of ice cover is expected to increase (Sharma et al., 2015).

5.2 | Precipitation events

While most lakes are sensitive to nutrient pulses, oligotrophic lakes are especially susceptible due to their more severe nutrient limitation. Rigosi et al. (2014) analysed more than 1,000 lakes in the contiguous U.S.A. and found that oligotrophic lakes were more susceptible to increases in the relative abundance of cyanobacteria from increased nutrients alone, while mesotrophic lakes were more impacted by temperature, and eutrophic lakes were most affected by the concomitant effects of nutrients and temperature. An increased frequency in major precipitation events and associated run-off events provides sporadic inputs of limiting nutrients to oligotrophic systems (Jeppesen et al., 2009; Sterner et al., 2020), which may be used directly or stored by cyanobacteria for later use. Nõges et al. (2011) found that chlorophyll increased in an oligotrophic lake following a rainy winter period, while cyanobacterial blooms were disrupted in a nearby eutrophic lake due a change in phytoplankton community composition toward a higher abundance of diatoms, chlorophytes, and chrysophytes. Pulses of limiting nutrients are capable of modifying seasonal phytoplankton succession, re-selecting for fast-growing phytoplankton and organisms capable of storing nutrients (Piovia-Scott et al., 2017; Stockwell et al., 2020). While high discharge can affect cyanobacterial biomass in both positive (higher nutrient input) and negative (flushing, destratification) ways, the more severe nutrient limitation in oligotrophic lakes may favour positive effects on cyanobacteria. These effects of increased nutrient pulses delivered during high-intensity precipitation events may be amplified by higher temperatures, thus increasing cyanobacterial growth (Lürling et al., 2018).

5.3 | Catchment land-use and nutrients

Future changes in land use in conjunction with more frequent intense precipitation events are expected to have profound impacts on the timing and rates of in-lake processes. The conversion of catchment forests to agricultural or urban land-use practices can ultimately lead to increased cyanobacterial blooms in lakes (Brookes & Carey, 2011). The proportion of catchment cropland is positively correlated with cyanobacterial biomass, while proportions of catchment forest tend to be negatively correlated with cyanobacterial blooms and cyanotoxin concentrations at regional and continental scales (Beaver et al., 2018; Doubek et al., 2015). Deforestation within oligotrophic lake catchments promotes nutrient loading and sedimentation into lakes (Stoddard et al., 2016). Moreover, increased use of glyphosate-based herbicides or other nutrient-containing chemicals in the basin leads to increased organic nutrient forms in downstream water bodies, which are preferentially utilised by cyanobacteria compared to eukaryotic algae (Harris & Smith, 2016). A combination of deforestation and increases in urban and agricultural land use may ultimately cause increases in potentially growth-limiting labile nutrients or metal forms (e.g. Fe) that promote cyanobacterial blooms in macronutrient and trace metal limited oligotrophic systems.

5.4 | Multiple factors affecting Fe

Additional knock-on effects from changes to climate, precipitation patterns, catchment land-use, and nutrients include several factors that are likely to increase access to reduced Fe (Molot et al., 2021), which can promote cyanobacterial growth. While increased water temperatures alone are probably insufficient to lead to cyanobacterial dominance in most lakes, the combination of warm waters and anoxic sediments that release Fe are sufficient even in oligotrophic lakes (Verschoor et al., 2017). Higher water temperatures increase microbial activity that increases the risk and duration of anoxia at the sediment-water interface and thus increases the likelihood of Fe release into the water column. Long ice-free seasons (Sharma et al., 2019) allow for longer periods of oxygen loss and thus increased risk of anoxia in the hypolimnion. This is particularly true in autumn when surface waters are still warm (Li et al., 2018). Higher air temperatures, longer ice-free seasons, and increased low-wind periods permit shallow polymictic lakes to develop thermal and oxygen gradients more often and thus increase reduced Fe flux from sediments to the water (Jabbari et al., 2019). Wetter springs and the large nutrient loads they bring result in larger blooms that persist for longer periods (e.g. Lake Erie, Stumpf et al., 2016). Increased hydrologic connectivity in wetter springs also leads to increased bloom activity (e.g. Lake Winnipeg, Ali & English, 2019).

6 | MANAGEMENT AND FUTURE DIRECTIONS

Managing the risk of cyanobacterial blooms in oligotrophic lakes requires a tailored approach. Strategies for nutrient reduction in already oligotrophic environments are unlikely to effectively mitigate nuisance blooms; however, maintaining low nutrient concentrations in inflows should remain a priority, and more attention should be paid to climate-driven nutrient pulses (e.g. precipitation, Morabito et al., 2018 and wind, Thyssen et al., 2014) releasing systems from nutrient-depleted conditions in the short term and potentially leading to undesired phytoplankton blooms. Advising the public of risks, adjusting water withdrawal depth away from surface and metalimnetic accumulations, and increasing monitoring of surface blooms through manual sampling/visualisation or remote sensing is a prudent response. Most management methods have been developed based on single or dual nutrient abatement applied externally (e.g. land-use management) and internally (e.g. application of P-locking agents that precipitate P and block P in the sediments from releasing, Lürling et al., 2016) to counteract eutrophication-fuelled blooms, but some other in-lake approaches that do not directly target nutrients but rather target the nuisance algae could be more effective in oligotrophic systems such as algaecides (e.g. hydrogen peroxide), flocculation and coagulation of algae cells (Liu et al., 2013), artificial mixing to reduce light available for phytoplankton growth (Visser et al., 2016), or application of ultrasound (Wu et al., 2011) that leads to rupture of gas vesicles and inhibit the growth of cyanobacteria. However, some of these techniques have been shown ineffective for controlling cyanobacteria (e.g. ultrasound in Lürling & Tolman, 2014 and mixing in Lürling et al., 2016, Visser et al., 2016) and restoration techniques that work well in the current climate may not be effective in the future (Jeppesen et al., 2009). It is important that we continue to develop and evaluate new management techniques that work efficiently in oligotrophic systems and under future climate scenarios.

We recommend that future work include more consideration of biological traits and abiotic processes that give rise to cyanobacterial blooms that are not directly linked to nutrients in the water column. For instance, information on dormant cells (akinetes, vegetative cells) is very limited, and the conditions that lead to encystment and germination are poorly described in the literature. These processes may be critical in seeding blooms in low-nutrient systems where bloom forming conditions may not be present annually (Callieri et al., 2014). Additional work is also needed to describe hydrodynamic processes (e.g. currents, wave action including internal waves, and upwelling events) that give rise to blooms, as they may be particularly important in oligotrophic systems where the overall biomass concentration may be low, but abiotic conditions result in the concentration of biomass, and subsequent surface scums. Further, hydrodynamic processes may interplay with biological processes, such as suspending vegetative or resting stage cells in the sediments and initiating growth through exposure to nutrients and warmer temperatures in the water column. These are just a few examples of bloom ecology in oligotrophic lakes where knowledge is lacking because of the historical focus on eutrophic lakes. By shifting the high-nutrient paradigm to improve our understanding of cyanobacteria in low-nutrient lakes, we may be able to better manage and prevent blooms in oligotrophic systems.

7 | CONCLUSION

Cyanobacteria evolved in low-nutrient systems (Bjerrum & Canfield, 2002) and continue to thrive in oligotrophic systems. This has been largely overlooked as the spectacular blooms in eutrophic systems have grabbed headlines. To fully understand cyanobacterial ecology and effectively inform management strategies, we need to explore mechanisms that facilitate cyanobacterial growth, maintain biomass, and cause blooms to senesce across multiple trophic states. Cyanobacterial growth requires four factors: an inoculum, adequate light, temperature, and nutrients (Reynolds, 2006). If vegetative cells persist in the water column or germinate from akinetes then there is always a potential for growth. Light can limit the rate of growth, but not until large populations exist and shading, deep mixing (Ibelings & Maberly, 1998), or light reduction due to dissolved organic C or suspended sediment occurs. Nutrients can limit both the rate of growth and the total biomass (Carey, Ewing, et al., 2012). Oligotrophic lakes may have low nutrient concentrations but can still support sufficient standing cyanobacterial biomass to create scums through the various mechanisms described above.

Ultimately, physiological adaptations and lake physics create the conditions under which surface aggregations and metalimnetic maxima can occur in oligotrophic systems (Lofton et al., 2020). Specialised cells allow cyanobacteria to utilise nutrient pools that are unavailable to other phytoplankton, as well as take up and utilise nutrients more efficiently. Buoyancy provided by gas vesicles encourages surface bloom formation. While nutrient-limited cyanobacteria contain fewer gas vesicles and may have more ballast than their nutrient replete counterparts (Kromkamp, 1987), they can still be sufficiently buoyant to reach the water surface and become trapped there by surface tension (Hutchinson & Webster, 1994), or remain in the metalimnion near hypolimnetic nutrients. Although cyanobacteria may have a low average biomass, the accumulation of cells in a surface bloom or scum and the concomitant concentration of toxins and taste and odour compounds are of concern for recreation and water supply. As the intensity and duration of thermal stratification are expected to continue to increase (Woolway et al., 2020), the physical conditions supporting cyanobacterial blooms in oligotrophic lakes may also become more prevalent, resulting in more oligotrophic blooms in the future.

In summary, we propose that climate change processes including lake warming, increased water column stability, and increased frequency and intensity of storm events will probably favour cyanobacterial blooms in *both* oligotrophic and eutrophic lakes. Cyanobacteria have numerous physiological adaptations that allow them to outcompete other primary producers across a wide range of physicochemical conditions. Our working model for mitigating blooms, however, is to reduce eutrophication and as such, we have largely overlooked cyanobacterial blooms in oligotrophic lakes. Here, we show that physical, biological, and chemical mechanisms driving cyanobacterial growth and biomass maintenance are shared across trophic states. Effective management and mitigation of cyanobacterial blooms thus require shifting our high-nutrient paradigm toward a trophic-gradient paradigm that includes a comprehensive understanding of how traits and physicochemical conditions interact to sustain blooms in a rapidly changing global climate.

DATA AVAILABILITY STATEMENT

No new data were used in the development of this manuscript. All published data can be found at the links and/or citations provided in the manuscript and supplementary text and tables.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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