

**Paradox vs. Paradigm: A Disconnect Between Understanding and Management of Freshwater  
Cyanobacterial Harmful Algae Blooms**

Andrew J. Bramburger<sup>1\*</sup>, Christopher T. Filstrup<sup>2</sup>, Euan D. Reavie<sup>2</sup>, Cody S. Sheik<sup>3</sup>,

G. Douglas Haffner<sup>4</sup>, David C. Depew<sup>1</sup>, John A. Downing<sup>3,5</sup>

1. Watershed Hydrology and Ecology Research Division, Water Science and Technology Directorate, Environment and Climate Change Canada. 867 Lakeshore Rd. Burlington ON, L7S 1A1, Canada.
2. Natural Resources Research Institute, University of Minnesota Duluth. 5013 Miller Trunk Highway, Duluth MN, 55811, USA
3. Large Lakes Observatory and Department of Biology, University of Minnesota Duluth. 2205 E 5th St., Duluth MN, 55811, USA
4. Great Lakes Institute for Environmental Research, University of Windsor. 401 Sunset Ave, Windsor ON. N9B 3P4, Canada.
5. Minnesota Sea Grant, University of Minnesota Duluth, 31 W. College Street, Chester Park Building, Duluth MN, 55812, USA

\*Corresponding author: [andrew.bramburger@canada.ca](mailto:andrew.bramburger@canada.ca)

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**Abstract**

1. Freshwater cyanobacterial harmful algae blooms (CHABs) are a major threat to human and environmental health and are increasing globally in frequency and severity. To manage this threat in a timely manner, science must focus on increasing our ability to predict the growth and toxigenicity of specific taxa of cyanobacteria.
2. Recent molecular research has revealed striking genomic and metabolic diversity among the many morphologically indistinguishable sub-species and strains of cyanobacteria. Assemblage-level molecular metabolic capability surveys promise to improve our ability to predict cyanobacterial responses to environmental forcing, but many of these cutting-edge techniques are not widely available or cost-effective enough to be employed in routine monitoring programs to support management decisions. Taxonomic ambiguity, cryptic functional specialization, incongruence between metabolic capability and phylogeny, and genomic flexibility impose severe challenges to our ability to ascribe autecological attributes at a level of taxonomic resolution that is attainable under current management strategies (i.e. Linnaean species). This lack of knowledge prohibits reliable predictions of species' responses to environmental stressors.
3. Cyanobacterial "species" comprise consortia of metabolically diverse, morphologically indistinct strains that span a range of ecological specialization. Under current, broadly applied taxonomic concepts, these species functionally embody a generalist ecological strategy – persisting and/or proliferating where other specialized competitors are negatively impacted.
4. We postulate that within current management frameworks, characterizing of cyanobacterial "species" as competing generalists, as well as considering abundance trajectories of well-characterized,

non-cyanobacterial specialist phytoplankton will generate more scalable, mechanistic, and management-relevant insight into increasing cHAB frequency and severity in suitable time frames.

5. Here we recommend that cHAB management consider the competitive framework of phytoplankton communities, including cyanobacteria, wherein diverse environmental changes lead to deterministic responses by readily-identifiable, documented specialist taxa. Characterizing these changes in community structure will quantify the relative importance of altered stressors and resource availability that can be exploited by metabolically flexible cyanobacteria.

## Introduction

Harmful algal blooms (HABs) are becoming more frequent in both freshwater and marine systems.

Although both pro- and eukaryotes may form HABs, events in freshwater ecosystems tend to be dominated by cyanobacteria (i.e. cHABs; Paerl et al., 2001), whereas marine blooms are characterized by representatives of the dinoflagellates, cryptophytes, chrysophytes, raphidophytes, diatoms, and cyanobacteria (Anderson et al, 2021). Freshwater cHABs represent a major threat to human and environmental health (Brooks et al., 2017) and have recently increased in frequency (O'Neil et al., 2012; Ho et al., 2019). The potential for public health impacts has sparked interest in research dedicated to cHAB prediction and mitigation (Wang et al., 2015; Li et al., 2017), supported by increased funding allocations (Lopez et al., 2008; Hudnell, 2010). However, cHABs have been reported with increasing frequency in freshwater systems regardless of thermal regime, trophic status, or anthropogenic impact (e.g. Winter et al., 2011; Favot et al., 2019; Sterner et al., 2020 Reinl et al., 2021), confounding investigators' efforts to understand the environmental forcing agents that facilitate cyanobacterial proliferation and trigger cHABS. Our attempts to predict and manage cHABs are further complicated by the application of an inappropriate species concept that often fails to capture the cryptic taxonomic and functional diversity *within* many cyanobacterial species (hereafter, the term "species" refers to morphologically-delineated Linnaean species) and cannot accommodate the dynamic nature of bacterial genomes. While cutting-edge molecular techniques promise to resolve cryptic sub-species diversity and help to elucidate the responses of cyanobacterial consortia to environmental stressors, it may be some time before these tools penetrate to routine monitoring and management programs on a broad scale. Even when taxa can be resolved, it is difficult to construct robust models that predict the onset, duration, and severity of cHABs in multiple systems. Thus there remains an immediate need for improved prediction of cHAB events in a wide diversity of freshwater systems (Pick, 2016). We recommend that consideration of broader phytoplankton community dynamics can help to detect rapid

environmental change and circumscribe ecological scenarios that might lead to the proliferation of cyanobacteria.

### **The Paradox of Cyanobacterial Proliferation**

While relationships between environmental drivers and algal density have been studied for decades (e.g. Vollenweider, 1968; Schindler, 1975), recent increases in reports of cHABs from diverse systems have prompted many investigators to ponder what has caused cyanobacteria to rapidly proliferate in systems spanning broad environmental gradients. Concern for public health has sparked considerable discourse on conditions that promote bloom initiation and toxin production (Roelke & Buyukates, 2001; Gilbert & Burkholder, 2018, Huisman et al., 2018). However, during the current period of environmental change, it is difficult to quantify the relative importance of multiple stressors in the ongoing shift towards cyanobacterial dominance. We propose that the cryptic functional diversity and inherent adaptability of cyanobacteria – products of their evolutionary history and genomic structure – have enabled them to capitalize on rapid change that has negatively impacted other phytoplankton.

Researchers have correlated cyanobacterial prevalence and cHAB occurrence with primary productivity (Downing et al., 2001), absolute nutrient concentrations (Downing et al., 2001), total phosphorus (P) concentrations (Schindler, 1977; Davis et al., 2009), nitrogen-to-phosphorus (N:P) ratios (Smith, 1983; Filstrup et al., 2016; Paerl et al., 2016), light (Havens et al., 2003), and water temperature (Paerl & Huisman, 2008; Beaulieu et al., 2013). Similarly, bloom initiation and toxin production onset have been linked to temperature (Hayes et al., 2020), water column stratification (Mullin et al., 2020), N speciation (Newell et al., 2019; Wagner et al., 2021), and water and cellular C-N-P stoichiometry (Van de Waal et al., 2014; Wagner et al. 2019). For example, many cyanobacterial taxa possess carbon concentrating mechanisms (CCMs) allowing them to thrive, relative to eukaryotic competitors, at low pCO<sub>2</sub> during periods of intense primary productivity (Morales-Williams et al. 2017, 2021). Similarly, diazotrophic

cyanobacteria are thought to gain a unique advantage in N-limited systems (Hayes et al., 2015; Harke et al. 2016). Measurable N-fixation under N-replete, P-limited conditions (Miller et al., 2013; Paerl & Otten, 2016, Natwora & Sheik, 2021), however, challenges the deterministic coupling of this physiological adaptation to broad stoichiometric gradients and highlights the functional diversity that can exist within aquatic microbial assemblages, including consortia dominated by cyanobacteria.

The current state of the science on freshwater cHABs poses the following paradox: How can cHABs attributed to (seemingly) so few species be triggered by such a variety of stressors in such a broad diversity of systems?

Cyanobacteria have existed in excess of 3.6BY (Garcia-Pichel et al., 2019) and have fundamentally experienced all combinations of environmental conditions - from the cryosphere (Quesada & Vincent, 2012) to geothermal hot springs (Rastogi et al., 2012) to hypersaline lakes (Oren, 2015). Despite the broad diversity of systems that have experienced recent increases in cHAB occurrence, including those that are cold (Sternner et al., 2020), oligotrophic (Favot et al., 2019, Reinl et al., 2021), and otherwise anthropogenically un-impacted (Winter et al., 2011), only a handful of species have been implicated in these events. This phenomenon is a consequence of extensive cryptic taxonomic diversity and metabolic specialization *within* cyanobacterial species. Like other prokaryotes, cyanobacterial species comprise numerous morphologically indistinguishable strains with marked genomic and physiological differences (Dvořák et al., 2015). The Laurentian Great Lakes provide a good illustration of cyanobacterial distribution across broad ecological gradients. While eutrophic Lake Erie is much more productive than the other Great Lakes, the genera most often associated with cHABs (often the same handful of species) occur across all 5 lakes (Fig.1), with relatively consistent summer epilimnetic biovolume, when averaged across stations by lake. The occurrence of these “usual suspects” across all 5 lakes demonstrates the tolerance of cyanobacteria to widely divergent temperatures and trophic states. For example, the strain

of *Dolichospermum* (formerly *Anabaena*) *lemmermannii* (Fig. 2) that dominated the 2018 bloom cold, oligotrophic Lake Superior (Sterner et al., 2020, Reinl et al., 2021; Sheik et al. 2022) is commonly reported in the lower Great Lakes, including Lake Erie). It has also been associated with cHABs in warm, eutrophic western Lake Erie (Driscoll et al., 2018; Sheik et al., 2022) and brackish waters in coastal Finland (Driscoll et al. 2018). *D. lemmermannii* comprises multiple morphologically indistinct strains that exhibit considerable metabolic heterogeneity (Sheik et al. 2022), including multiple pathways for nutrient assimilation, transport, and storage, defenses against photodamage and oxidative stress, and synthesis of bioactive compounds including toxins (Österholm et al., 2020).

The structure of the cyanobacterial genome reflects the evolutionary history of the phylum, and maintains metabolic flexibility and supports rapid evolution. Like those of eukaryotic algae, cyanobacterial genomes consist of a relatively stable core set of genes, conserved across deep-branching evolutionary lineages, that regulate critical cell processes (photosystems, cell-cycle regulation, genome replication, etc.). Unlike eukaryotes, cyanobacteria possess a dynamic suite of accessory genes that control auxiliary processes (nutrient scavenging, buoyancy control, toxin production, etc.; Shi & Falkowski, 2008; Alvarenga et al., 2017). Evolutionary conservation of core genes is driven by cellular necessity, and complex interactions among the structures and pathways encoded therein likely confer resistance against piecemeal horizontal gene transfer (HGT; Shi & Falkowski, 2008). In contrast, the genes regulating the multitude of processes supporting and augmenting chlorophyll- $\alpha$  mediated photosynthesis vary among taxa (including among cryptic strains) and confer subtle ecological differences that can facilitate coexistence of multiple taxa (per Hutchinson, 1961). These accessory portions of the genome are more plastic and can gain genes and functionality via HGT and/or viral integration. Genome rearrangements, transposon insertions, and gene loss also contribute to remarkable intraspecific genome diversification and sub-speciation (Prabha et al., 2016), as well as the potential for rapid transmogification of metabolic capacities within lineages.

Considering their lengthy evolutionary history and relatively dynamic consortium-level genomics, the relatively small number of cyanobacterial species that have been implicated in the recent increase in CHAB events are more accurately characterized as a number of cryptic taxa exhibiting broad metabolic diversity. Further, cryptic genotype diversity supports persistence of sub-species strains during environmental stress, allowing species to effectively sidestep extinction due to selective bottlenecks, and facilitating expeditious adaptive responses to rapidly changing conditions (Frangeul et al., 2008). The broader “rise of the cyanobacteria” in response to a seemingly wide variety of stressors is a consequence of the virtually limitless potential rearrangements of the cyanobacterial pan-genome. This suggests that current taxonomic approaches that are widely applied in monitoring lack sufficient resolution to support robust predictions of cyanobacterial proliferation and CHAB occurrence.

#### **The (Flawed) Paradigm of Managing Cyanobacteria as Linnaean Species**

Algae are classified into divisions based on their characteristic photosynthetic pigments, and further differentiated by morphology and habitat (Brodie & Lewis, 2007). As advances in microscopy facilitated improved taxonomic resolution, investigators described myriad morphotypes, with many circumscribed under Linnaean species epithets. Despite belonging to a different domain, (Bacteria as opposed to Eukaryota), cyanobacteria have traditionally been considered alongside their eukaryotic counterparts as aquatic photoautotrophs, and cyanobacterial ecology has been addressed in a similar fashion to that of other algae. For example, Reynolds (1997) placed cyanobacteria-dominated functional groups (e.g., *Microcystis*-dominated Groups Lm, M) alongside diatom-dominated groups (e.g., Group P) based on energy and resource limitation axes. However, cyanobacterial species are neither systematically nor evolutionarily equivalent to eukaryotic algal species. Application of Linnaean species classifications and morphospecies concepts are not appropriate for this group and do not accommodate recent molecular insights into the metabolic capabilities of sub-species strains or consortia of cyanobacterial taxa.



In eukaryotic lineages, evolutionary transfers of non-photosynthetic genes into the well-protected nuclear genome are thought to have resulted in infrequent HGT and therefore reduced incongruence between morphology and function (Shi & Falkowski, 2008). While locally-adapted populations do exist, the autecology of Linnaean morpho-species is relatively temporally and spatially consistent among many eukaryotic algae, forming the basis for fields such as diatom paleoecology (e.g., Dixit et al., 1992).

Contrastingly, each nominal cyanobacterial species likely represents an amalgam of strains and the same species may thrive and bloom in markedly different systems (e.g. oligotrophic vs. eutrophic). These distributional characteristics, coupled with the challenges of cyanobacterial systematics, make it difficult to ascribe metabolic function and autecology at current levels of taxonomic resolution, and accordingly prohibit reliable predictions of species' responses to environmental drivers.

Despite this, management of cHABs in freshwater systems remains largely based upon the characterization of "ideal" conditions for growth, proliferation, and toxin production of cyanobacteria at the species level, often focusing primarily on temperature and nutrient concentration and bioavailability (Przytulksa et al., 2017; Ho & Michalak, 2020; Paerl & Barnard, 2020). Recent molecular work (e.g. full-genome sequencing, metabolic pathway reconstruction) has resolved some taxonomic discord and provided insight into the metabolic capabilities of particular strains of interest (e.g. Dittman et al., 2015; Sheik et al. 2022), but insights from cutting-edge cHAB research have proven difficult to reconcile with broadly applied taxonomic concepts. In some cases, single-strain optima are attributed to entire species comprised of multiple morphologically similar strains. Further, while individual strains can proliferate under specific conditions, genomic variations are particularly incongruent with molecular phylogeny in this division (Mikalsen et al., 2003; Shi & Falkowski, 2008; Yerrapragada et al., 2009; Dvořák et al., 2015) and further confounds our ability to ascribe particular metabolic capabilities (e.g. toxin production) at the species level. Consequently, this current approach has not generated scalable, applicable tools for the management of globally increasing cHAB frequency and severity, although it has yielded useful

models for predicting bloom severity according to nutrient inputs in perennially susceptible systems (e.g. Lake Erie, Taihu; Watson et al., 2016; Huisman et al., 2018).

One potential solution to these issues would be to abandon attempts to predict taxon-specific responses and instead quantify consortium-level genomic capabilities and gene expression. In consortia of marine microbes, investigators have used recently-developed metagenomics approaches and metabolic pathway profiling to catalogue the metabolic diversity of the marine microbial community (Kennedy et al., 2010) and describe relationships in which the functional components of metabolic pathways are partitioned among taxa within the consortium. These consortia are capable of complex ecological processes including the breakdown of diesel contamination (Tiralerdpanich et al., 2018) and degrading highly persistent organic compounds including polycyclic aromatic hydrocarbons. In consortia containing marine cyanobacteria, variable gene expression among taxa, particularly in N-cycling genes, suggest that different organisms fulfill different roles in consortium-level nutrient cycling processes (Steppe et al., 1996; Thompson & Zehr, 2013; Lee et al., 2018). In these cases, the frequency and expression of key functional genes is a better predictor of metabolic and ecological function than presence or relative abundance of species within the assemblage. Alvarenga et al. (2017) suggested the value of consortium-based metagenomic explorations of cHABs, and indeed several investigators have examined cHABs from a metagenomic perspective. Pope & Patel (2008) demonstrated that freshwater cHABs could contain representatives from several bacterial phyla, while McCarthy et al. (2007), Louati et al. (2015), Li et al. (2020), and Pound et al. (2021) illustrated that cHAB-forming taxa often rely upon heterotrophic bacterioplankton to recycle nutrients within blooms. Following these studies, it may be possible to generate reliable predictions of cHAB initiation and toxin production by examining relationships between environmental stressors and gene frequency and expression.

Unfortunately, metagenomic and metatranscriptomic techniques remain too costly to be deployed at the scale and frequency required for most monitoring programs. They also pose technical and logistical challenges that render them unreliable in the absence of specialized infrastructure and highly trained personnel. As such, it will be many years before these approaches are widely accessible. With freshwaters that provide recreational opportunities and drinking source water increasingly threatened by cHABs, there is an immediate need to improve predictions of cHAB onset to protect public health and prevent economic, ecological, or aesthetic dysfunction (Chorus and Welker 2021). While cHAB management is largely saddled with an inappropriate species concept and cutting-edge techniques remain unavailable, there is a wealth of robust distributional and autecological data collected for eukaryotic phytoplankton by many ongoing biological monitoring programs. We propose that these datasets can be leveraged to identify indicator taxa that occur concurrently with – or immediately preceding – cHABs, thereby improving our predictive capacity for cHAB events.

### **(Re) Integrating cHAB Management into the Broader Field of Phycology**

The perspectives of cyanobacterial species as monophyletic generalists or polyphyletic consortia of cryptic specialists bear similar implications for cHAB management in the near term. Reliable prediction of response to stressors and management actions is virtually impossible under current, broadly applied taxonomic concepts that fail to resolve morphologically indistinct strains. Therefore, if we continue to apply morphology/microscopy based Linnaean taxonomic constructs, many species within the phylum Cyanobacteria should be managed as functional ecological generalists. While they might proliferate under specific environmental conditions (“optima”), their cryptic functional diversity and broad tolerance facilitates their persistence and ubiquity, particularly during periods of environmental change. While cutting-edge molecular techniques will eventually help to resolve cryptic taxonomy and clarify cyanobacterial responses to environmental drivers, current needs to protect public health have

stimulated ongoing management-targeted research that has focused on determining autecological optima for a handful of potentially harmful species and their constituent strains (Ibelings et al., 2016; Chorus and Welker, 2021). Often, these studies are conducted in vitro upon axenic cultures (Alvarenga et al., 2017). This cyanobacterial strain-centric approach diverges from foundational research on phytoplankton community dynamics that includes cyanobacteria in broader assemblages (e.g., Hutchinson, 1961; Sommer et al., 1986, 2012; Reynolds, 1997) as well as recent consortium level work that explores cyanobacterial-microbe metabolic interactions that may contribute to bloom phenology (McCarthy et al., 2007 ; Louati et al., 2015; Li et al., 2020; Pound et al., 2021). Despite the existence of optima for individual strains, functional incongruency with molecular phylogeny in this division (Shi & Falkowski, 2008; Yerrapragada et al., 2009; Dvořák et al., 2015) further challenges response predictions at management-relevant levels of taxonomic resolution. Here, we suggest that consideration of these broader community dynamics, in particular competitive interactions with non-cyanobacterial algae exhibiting well-supported deterministic relationships to environmental conditions, would help to constrain the uncertainty surrounding potential cyanobacterial responses to environmental drivers.

In freshwaters, cyanobacteria occur alongside eukaryotic algae across broad trophic gradients (Beaver et al., 2018) and even during intense cHABs, do not exist as monocultures (Anderson et al., 2002; Berry et al., 2017). Interactions such as competition for light and nutrients between cyanobacteria and eukaryotic phytoplankton influence bloom phenology and dynamics. During blooms, understory cyanobacteria and eukaryotic algae play a role in bloom development and nutrient cycling (Liu et al., 2019). For instance, dramatic satellite images depict cyanobacterial blooms in western Lake Erie as relatively uniform entities (Michalak et al. 2013), but they are actually complex, spatially heterogeneous assemblages including diatoms and other phyla (Reavie et al. 2014). This implies that resource utilization by cyanobacteria is regulated in part by interactions with eukaryotic algae (and vice versa). Despite our growing knowledge of cyanobacterial metabolic capabilities, resource tolerances, and optima,

taxonomic ambiguity challenges our ability to predict ecological outcomes in multi-strain consortia, and our understanding of their interactions with other phytoplankton is considerably limited (Neilan et al., 2013). Similarly, niche breadths and positions inferred from laboratory studies represent fundamental niches (per Roughgarden, 1974) of individual strains, rather than variable, realized niches (per Hutchinson, 1957, 1965) of polyphyletic species interacting within diverse phytoplankton assemblages. This also applies to similar studies focusing on eukaryotic taxa, but the issue is exacerbated by complicated taxonomy among cyanobacteria. As such, circumscriptions of the realized niches of CHAB-forming taxa (or consortia) can be made more robust by quantifying resource use by competing taxa.

We can better characterize the conditions that support the expansion of generalist species (or constituent strains representing consortia of cryptic specialists) by examining the gain and loss terms of more easily identifiable, known specialists. Levins (1968) argued that tradeoffs exist between ecological specialization and generalization wherein generalists are prone to be excluded by specialist competitors under stable, favorable (for the specialist) environmental conditions, but can survive under a wider range of conditions. In other words, a generalist strategy effectively minimizes loss terms (e.g. due to sinking, grazing, nutrient deficiency) across broad ecological gradients, while a specialist strategy maximizes growth terms under specific sets of conditions. Subtle ecological differences among taxa can facilitate coexistence (Hutchinson, 1961) provided there is enough environmental heterogeneity to preclude competitive exclusion of less well-suited taxa (Richerson et al., 1970). Algal communities are no exception to this trend (see Bramburger et al., 2020a), and realized niches of generalists or functionally ambiguous consortia are constrained by competitive interactions with specialists.

Cyanobacteria compete for resources within communities alongside eukaryotic algae. Despite some metabolic and functional abilities that are unique to cyanobacteria (Hyenstrand et al., 1998), the considerable niche overlap existing along core resource gradients is substantiated by both evolutionary

history and genomic data. For example, the plastids of eukaryotic algae and plants likely arose through engulfment and endosymbiosis of a cyanobacteria-like organism by an early heterotroph ~1.5 BYA (Margulis, 1970; De Alda et al., 2014). Consequently, the molecular underpinnings of the major photosystems, including HGT-resistant gene clusters, are highly conserved among cyanobacterial core and eukaryotic plastid genomes (Shi et al., 2005), meaning that mechanistic responses of primary photosynthetic pigment, chlorophyll  $\alpha$ , to light are axiomatically uniform among divisions and foment intense interspecific competition. However, competitive outcomes for light are often influenced by tolerances to stressors regulating the multitude of processes that support and augment chlorophyll  $\alpha$ -mediated photosynthesis (auxiliary pigmentation, nutrient assimilation, buoyancy control, etc.). While taxonomic ambiguity, metabolic flexibility, and phylogenetic/functional incongruence make these relationships difficult to resolve for cyanobacterial species, we can capitalize on a wealth of eukaryotic phytoplankton occurrence and autecological data to rapidly identify conditions that may be conducive to cyanobacterial proliferation.

Many eukaryotic algae provide a ready means for circumscribing ecological conditions, and this approach is well-supported in the literature. Among the diatoms, in particular, there are many species that are easily identified under light microscopy and exhibit high fidelity to environmental stressors across broad geographic distributions (Dixit and Smol, 1994; Smol and Cumming 2000). As with selection of taxa to include in models to assess environmental quality or infer paleo conditions, investigators must be rigorous in their evaluation of species response relationships to stressors (in this case co-occurrence with CHAB-forming taxa or conditions that precede CHAB onset). Reliable indicators are characterized by strong relationships with stressors that are minimally confounded by extraneous environmental variables (Reavie and Cai, 2019). Abundances of these species – often typifying a *K*-selected ecological strategy (per Wilson and MacArthur, 1967; Bramburger et al., 2020a) characterized by relatively slow growth rates – are influenced heavily by loss mechanisms. They are therefore subject to decline in

abundance during unfavorable conditions, and are not likely to proliferate expeditiously in response to rapidly changing resource availability. Many systems undergoing recent increases in cHAB occurrences are not warm, eutrophic, or otherwise anthropogenically impaired in an absolute sense (e.g. Röhland et al., 2010). These systems have, however, undergone rapid environmental change and associated declines in previously dominant phytoplankton taxa (Box 1), suggesting that relationships between cHABs and environmental drivers are often associated with direct responses of specialist taxa.

Similar to phytoplankton-based inferences of phosphorus concentration, turbidity, or other aspects of environmental condition, trends in the abundance of taxa that decline prior to cHAB events or persist alongside bloom-forming cyanobacteria can provide insight into the susceptibility of a system to cyanobacterial proliferation. For instance, in many temperate lakes, stratified conditions occur in only a small fraction of the year, and ice-covered and isothermal seasons support phytoplankton communities dominated by large centric diatoms (Bondarenko et al., 2006; Twiss et al., 2012; Reavie et al., 2016). Not unlike destruction of established tree populations by forest fire, decreasing epilimnetic water density and cessation of turbulent mixing during the rapid onset of summer stratification represent disturbances that clear the epilimnion of standing diatom crops (via sinking; Winder et al., 2009; Bramburger and Reavie, 2016), freeing space and resources for use by generalist species (or constituent cryptic specialist strains) who do not require turbulent water column conditions, including Cyanobacteria. By tracking the biomass, composition, and loss rate of specialist diatoms (e.g. *Aulacoseira islandica*, which dominates late-winter/early spring sympagic and turnover communities), we can better predict the timing and magnitude of resource re-allocation. In the Laurentian Great Lakes, declines of large, specialist diatom taxa have coincided with the recent rise of cyanobacteria (Bramburger et al., 2017, 2020b). In western Lake Erie, a recent increase in the frequency of highly-visible cHABs has caused many to assume the lake's productivity has increased over the last few decades, and the lake has returned to the eutrophic state it exhibited in the mid-20th century. However,

water-column integrated measures of biomass, chlorophyll  $\alpha$ , and carbon-assimilation show that while the taxonomic makeup of the phytoplankton community of Lake Erie has changed, its biomass and primary productivity have remained relatively unchanged since the early 1970s (Table 1). In cHAB-prone years, the bulk of the summer phytoplankton biomass has been concentrated within the upper epilimnion, where cyanobacteria tend to replace less buoyant taxa, like diatoms. Loss of diatoms from the water column is not the only mechanism that can change resource availability for cyanobacteria. Similar opportunities generated by rapid increases in available nutrients (Hecky et al., 2010; Schindler et al., 2012), increasing variability (pulsing) of nutrient delivery precipitating periods of “feast-or-famine” for pre-existing communities (Sommer, 1985), or altered loss rates due to changing grazing pressure (Smith et al., 2005) can also be exploited by metabolically flexible, rapidly growing species.

While the toxic potential of a bloom can be inferred by assessing the frequency of toxin genes or the ratio of toxic to non-toxic cells in the assemblage (Dziallas et al., 2011), it is difficult to predict the onset of toxin production. Predictions of the onset of toxigenesis are another area that could be improved by considering broader community structure, since expression of toxins by Cyanobacteria is partly influenced by the presence of other taxa. The primary function of these compounds is poorly understood, and further complicated by the fact that toxigenic cyanobacteria don't always produce toxins, even during active blooms (Ouellette & Wilhelm, 2003). The synthesis of cyanotoxins arose prior to the evolution of metazoan grazers (Schatz et al., 2007), suggesting that defense against zooplankton grazing is not their primary purpose (Paerl & Millie, 1996). Cyanotoxins are potentially an important class of secondary metabolites that confer competitive advantages during fluctuating environmental conditions (Holland & Kinnear, 2013; Downing et al., 2015). There is also growing evidence that effects of these compounds upon other taxa are not simply allelopathic. Cylindrospermopsin can stimulate protein phosphatase expression in some eukaryotic algae (Bar-Yosef et al., 2010), thereby increasing readily accessible P resources. This implies that our understanding of anthropocentrically important



facets of cHAB biology (bloom proliferation, toxin production) is incomplete if we discount ecological opportunities emanating from assemblage-scale phytoplankton dynamics.

Several investigators have begun to consider the implications of broader interactions for cHABs.

McCarthy et al. (2007), Louati et al. (2015), Li et al. (2020), and Pound et al. (2021) illustrated that cHAB-forming taxa often rely upon heterotrophic bacterioplankton to recycle nutrients within blooms, while Šulčius et al. (2018) and McKindles et al. (2020) showed that cyanophage infections and associated lysis of cyanobacterial cells often instigate the release of cyanotoxins into water columns. Cyanophages are also an important vector for the transfer of genetic material among cyanobacteria, implying that viral transfer probably contributed to novel appearances of toxigenesis in previously non-toxigenic strains (Mikalsen et al., 2003). While these innovations have contributed to a more holistic understanding of cHAB dynamics, few studies have considered direct or indirect effects of broader phytoplankton community structure.

While it is widely thought that cyanobacterial dominance and recurrent cHABs are hallmarks of stressed aquatic systems, we suggest that prediction of these phenomena based solely upon abiotic environmental drivers is at best problematic. Alternatively, we propose the following conceptual framework for understanding cyanobacterial proliferation and associated cHAB events on ecological and evolutionary timescales:

**Environmental change (perturbation) → Deterministic response by readily quantifiable specialist taxa  
→ Novel ecological opportunity (resource re-allocation) → Opportunistic response by cyanobacterial species (or constituent strains)**

We argue that the concurrent, ubiquitous emergence of optimal conditions for innumerable cyanobacterial strains is unlikely. Rather, the observed “rise of cyanobacteria” is a consequence of

cyanobacterial response to variations in the intensity of competition with specialist eukaryotic taxa under rapidly changing conditions. This global phytoplankton community restructuring at broad levels of taxonomy is a matter of niche breadth (tolerance and cryptic diversity) and not niche position (optima). In short, to better predict cyanobacterial and cHAB dynamics in a management-relevant context, we need to focus not only on what cyanobacterial species “like,” but also on what other phytoplankton “can’t handle.”

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**Figure Legend:**

Fig. 1 Mean lakewide summer epilimnetic biovolume of common CHAB-forming genera in the Laurentian Great Lakes, based on USEPA-GLNPO Great Lakes Biological Monitoring Program survey data (2001-2019; lakewide station totals).

Fig. 2: Putative *Dolichospermum lemmermannii* from 2018 bloom in L. Superior. Image: E. Alexson, University of Minnesota Duluth.

**Table 1:** Western Lake Erie temporal trends in phytoplankton biomass, chlorophyll *a*, net primary productivity, and relative cyanobacterial biovolume (Munawar & Munawar, 1976; Dahl et al., 1995; Smith et al., 2005; Porta et al., 2005; Fitzpatrick et al., 2007; Hillis, 2017; Owen 2019, USEPA-GLNPO unpublished data).

	1970	1993	1997	2001	2002	2003	2014	2015	2016	2017
Biomass ( $\text{g}\cdot\text{m}^{-3}$ )	4.5	0.8	-	4.6	-	-	2.8	1.6	4.5	5.6
Chl- <i>a</i> ( $\text{mg}\cdot\text{m}^{-3}$ )	11.4	4.1	5.7	9.0	4.2	7.2	4.7	3.5	8.2	2.0
Net primary productivity ( $\text{mgC}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ )	146	94	88	188	135	27	23	26	-	-
Summer relative Cyanobacterial biovol. (%)	-	-	7.2	7.3	19.7	4.0	69.3	74.5	41.0	45.1

Fig. 1

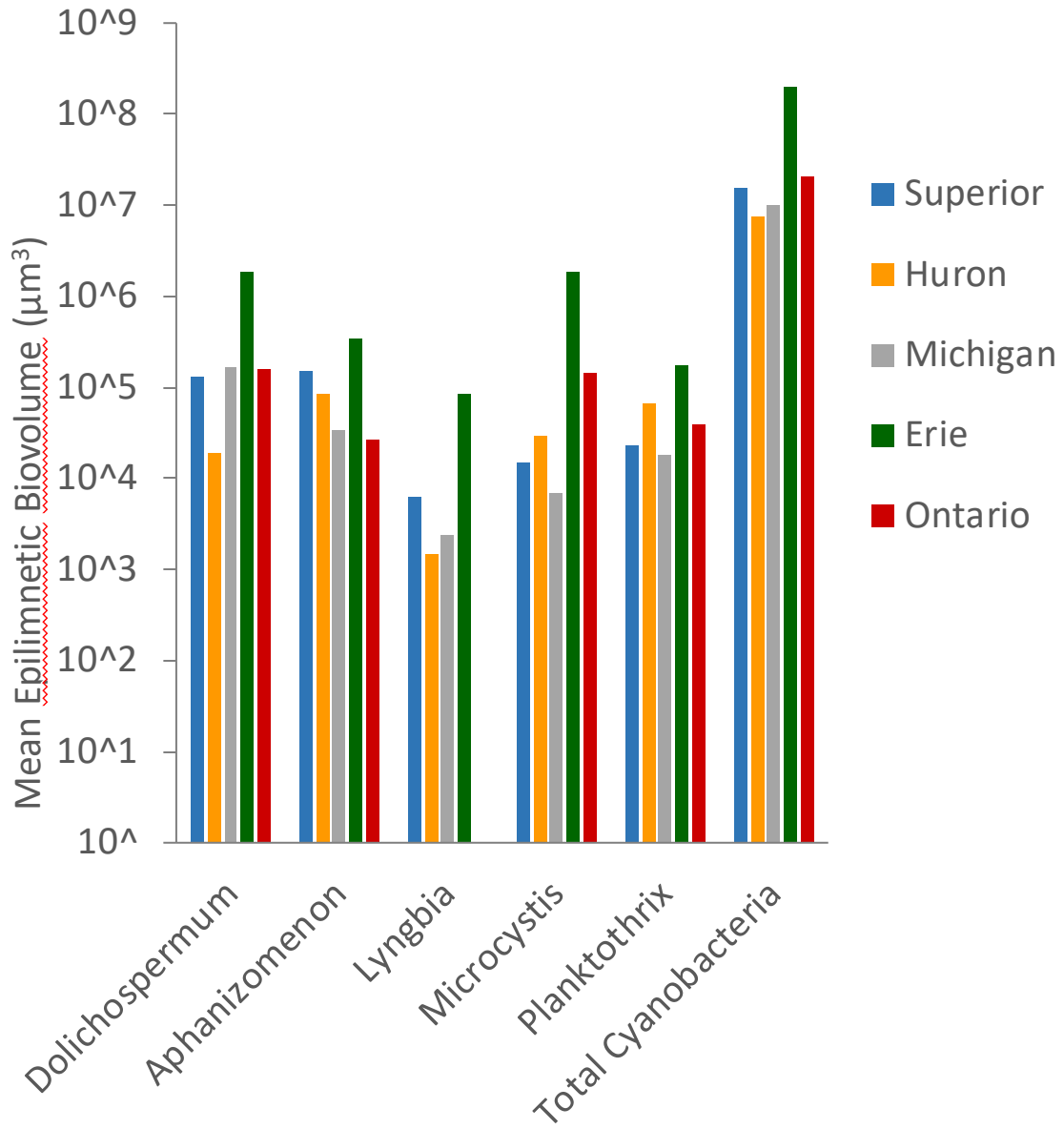
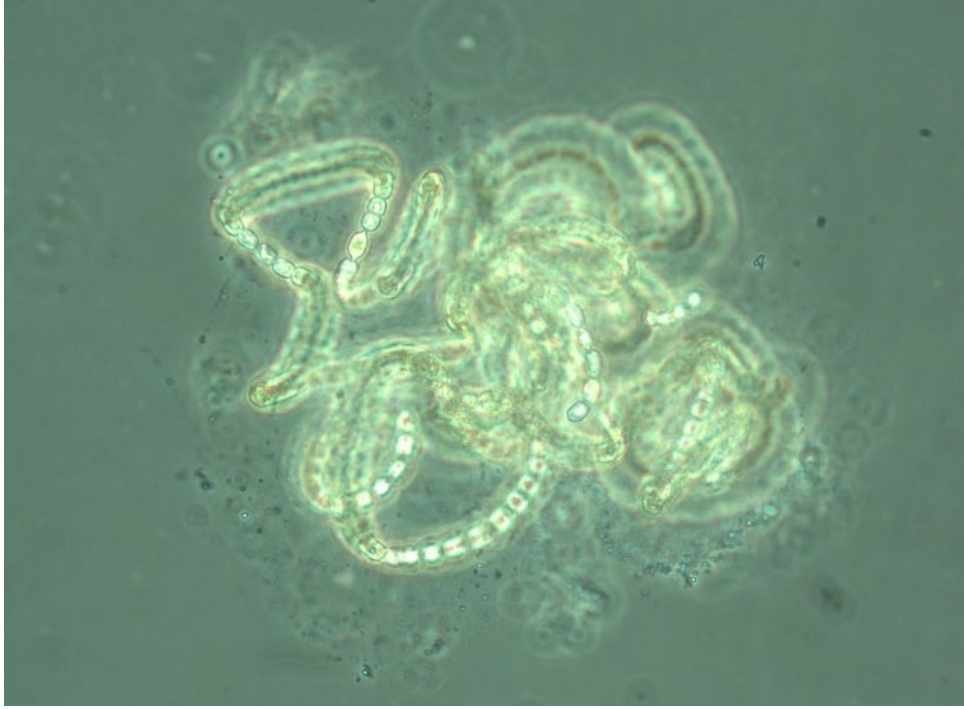
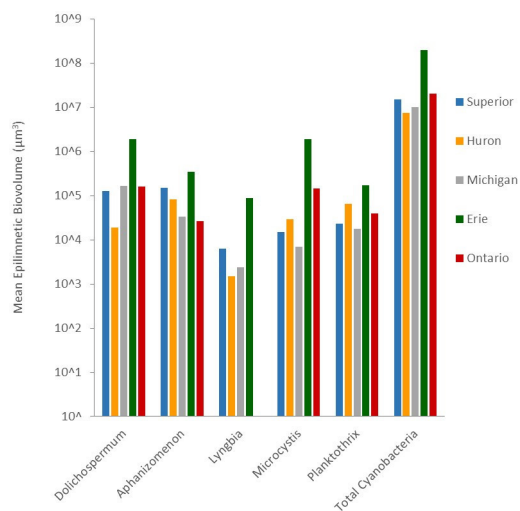
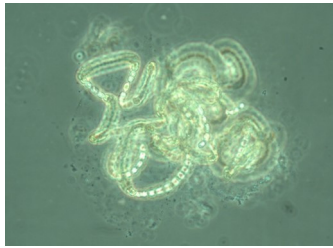


Fig. 2





FWB\_14019\_CHAB Fig 1.jpg



FWB\_14019\_cHAB fig. 2.jpg