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Review

A tale of two blooms: do ecological paradigms for algal bloom success and succession require revisiting?

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ABSTRACT

Lake Erie algal bloom discussions have historically focused on cyanobacteria, with foundational "blooms like it hot" and "high nutrient" paradigms considered as primary drivers behind cyanobacterial bloom success. Yet, recent surveys have rediscovered winter-spring diatom blooms, introducing another key player in the Lake Erie eutrophication and algal bloom story which has been historically overlooked. These blooms (summer *vs.* winter) have been treated as solitary events separated by spatial and temporal gradients. However, new evidence suggests they may not be so isolated, linked in a manner that manifests as an algal bloom cycle. Equally notable are the emerging reports of cyanobacterial blooms in cold and/or oligotrophic freshwaters, which have been interpreted by some as shifts in classical bloom paradigms. These emerging bloom reports have led many to ask "what *is* a bloom?". Furthermore, questioning classic paradigms has caused others to wonder if we are overlooking additional factors which constrain bloom success. In light of emerging data and ideas, we revisited foundational concepts within the context of Lake Erie algal blooms and derived five key take-aways: 1) Additional bloom-formers (diatoms) need to be included in Lake Erie algal discussions, 2) The term "bloom" must be reinforced with a clear definition and quantitative metrics for each event, 3) Algal blooms should not be studied solitarily, 4) Shifts in physiochemical conditions serve as an alternative interpretation to potential shifts in ecological paradigms, 5) Additional factors which constrain bloom success and succession (*i.e.*, pH and light) require consideration.

1. Introduction

Lake Erie (US/Canada) is an important North American resource: it provides potable water, supports regional ecosystems and serves as an economic resource to over 13 million basin residents (Fergen et al., 2022). On a global scale, the Laurentian Great Lakes are the largest continuous freshwater body on Earth, containing ~ 21% of the globe's surface freshwater (Botts and Krushelnicki, 1987). Yet, the ecological integrity of these lakes has been compromised by eutrophication and the return of harmful algal blooms in recent decades, with the most notably affected being Lake Erie (Steffen et al., 2014; Watson et al., 2016). As a result, Lake Erie serves as an ideal candidate for a case study revisitation of algal bloom principles and paradigms.

Due to the sheer visibility of summer cyanobacterial blooms, scientists and the popular press often view the western basin of Lake Erie as a summertime monoculture of *Microcystis* spp. While these often toxic cyanobacterial blooms deserve attention, the recent resurgence in awareness of winter-spring diatom blooms has introduced complexity to this precept. It is becoming increasingly evident that Lake Erie algal blooms are not just cyanobacteria and that other bloom-formers (notably diatoms) are overlooked. This exclusion is surprising; for albeit non-toxic, winter-spring diatom blooms do not come without ecological consequence. Prior studies suggest winter-spring diatom blooms can reach higher biovolumes and chlorophyll *a* (Chl *a*)

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concentrations than their summer cyanobacterial counterparts (Reavie et al., 2016; Twiss et al., 2012) and contribute significantly to summer hypoxia in the central basin of Lake Erie (Lashaway and Carrick, 2010; Reavie et al., 2016; Wilhelm et al., 2014). Because of these consequences, we propose winter-spring diatom blooms qualify as "harmful" algal bloom events (*vis a vis* Smayda, 1997). Yet, historically the community has been hesitant to definitively define them as such (Ozersky et al., 2021; Saxton et al., 2012; Twiss et al., 2012). We note there are additional bloom formers in Lake Erie (*e.g., Cladophora*) (Higgins et al., 2005), but our goal is to reassess the ecological success of the major summer (cyanobacteria) and winter-spring (diatom) bloom formers of this system.

Recent literature has indicated a need to revisit the age-old question "what *is* a bloom?" (Smayda, 1997). Blooms have traditionally been referred to as visible discoloration in the water column or as a surface scum (Huisman et al., 2018; Kalff, 2002). Yet, recent reports of "blooms" have led many to question the use of this term. For example, Reinl et al. (2023) reported 37 instances of cyanobacterial blooms in cold systems yet did not provide supporting quantitative metrics such as Chl *a* concentration, cellular abundance, *etc*. At least one case was likely not a bloom *per se*, rather a routinely observed abundant picocyanobacterial population (*Synechococcus* spp.) according to prior studies (Twiss et al., 2012; Wilhelm et al., 2006). Indeed, the limnological field at large has used "bloom" as an idiosyncratic and subjective term for decades (Ho and Michalak, 2015). Consequently, the term has become a qualitative sentiment rather than a quantitative diagnosis.

There is also a need to address successional linkages *between* summer cyanobacterial and winter-spring diatom blooms. The Lake Erie seasonal cycle suggests one bloom biogeochemically conditions the water column for the next (Wilhelm et al., 2020). In Lake Erie, carbon input from winter-spring diatom blooms enhances nutrient regeneration for summer events (Chaffin et al., 2018; Reavie et al., 2016). This linkage of winter-spring diatom and summer cyanobacterial blooms has been described elsewhere, including the Baltic Sea (Zilius et al., 2018) and smaller freshwater systems across the globe (Hampton et al., 2017), with the most recent being Petit-lac-Saint-François (Canada) (Julian et al., 2024). Addressing blooms as an integrated unit, rather than solitary events, may help resolve and further elucidate long-term bloom dynamics.

Recent literature has called into question the classic paradigms thought to constrain algal bloom success and succession (Reinl et al., 2021; Reinl et al., 2023). It has become a common mantra that cyanobacterial blooms "like it hot" (Paerl and Huisman, 2008), yet it has been recently proposed that blooms "also like it cold" (Reinl et al., 2023). Cyanobacteria have emerged in what were classically considered to be cold systems, such as Three Mile Lake (US) (Persaud et al., 2015) and Lake Baikal (Russia) (Namsaraev et al., 2018). In turn, the emergence of cyanobacterial blooms in large oligotrophic systems such as Lake Superior (US) (Sheik et al., 2022; Sterner et al., 2020) and smaller oligotrophic lakes such as Maggiore (Italy / Switzerland) (Callieri et al., 2014) and Hallwil (Switzerland) (Suarez et al., 2023) have been interpreted as a shift in the "high nutrient paradigm" (Reinl et al., 2021). A comprehensive revisitation of these paradigms is required in the face of emerging observations.

Novel data has suggested a need for a better understanding of phytoplankton competition and the role of additional drivers in algal success and succession. For example, recent research has characterized a role of cyanobacterial-induced elevated pH in the water column (*i.e.,* lake basification) in algal competition and succession (Shapiro, 1990; Zepernick et al., 2021; Zepernick et al., 2022b). Beyond biologically-driven lake basification, it has been projected anthropogenically-driven lake acidification may occur at the same rate as ocean acidification (Phillips et al., 2015). Yet, it remains to be determined how these pH shifts will affect freshwater communities. Light limitation is another trending topic within the field, with studies suggesting light availability exerts selective pressure on summer (Chaffin et al., 2014; Guildford et al., 2005; Jiang et al., 2015) and winter communities (Beall et al., 2016; Bramburger et al., 2023b; Zepernick et al., 2024). Based on these recent studies, there is a need to consider the contributions of additional drivers (*i.e.,* pH and light) to bloom success and succession.

Here, we focus on Lake Erie as a case study to revisit classic algal bloom paradigms, leveraging conclusions with recent literature spanning lakes of varying status, scale, and size. We re-evaluated the ecological success of Lake Erie's two principal algal blooms and revisited the age-old question "what *is* a bloom?" considering recent confusion and ambiguity regarding the term. Subsequently, we discussed the interlinkages of these two bloom events which form the Lake Erie seasonal bloom cycle (Wilhelm et al., 2020), and reexamined the paradigms for algal bloom success (temperature and nutrient status). Given lakes are sentinels of climate change (Adrian et al., 2009), there is a need to identify how algal blooms succeed across seasonal water columns to predict how climate change will alter current patterns. With this in mind, we note the paradigms discussed may apply to freshwater systems of all sizes beyond the Great Lakes. Conclusions of this revisitation include: 1) Additional Lake Erie bloom-formers (namely diatoms) need to be included in Lake Erie algal bloom discussions, 2) The term "bloom" must be used cautiously and reinforced with a clear definition and quantitative metric, 3) Algal blooms should not be studied in isolation from one another as they're implicitly linked, 4) Shifts in physiochemical conditions serve as an alternative interpretation to potential shifts in classic ecological paradigms, 5) Additional factors which constrain bloom success and succession (*i.e.,* pH and light) require additional attention.

2. Integrative discussions of Lake Erie algal blooms

Ecological success of Lake Erie cyanobacteria

Lake Erie has a history of summer cyanobacterial blooms throughout its western basin. We start by noting many cyanobacteria (*e.g., Synechococcus* and *Cyanobium* spp.) are routine components of a healthy lake system (Ivanikova et al., 2008; Wilhelm et al., 2006), while others are considered undesirable (*e.g.,* toxin producers). Cyanobacteria such as *Microcystis*, *Aphanizomenon* and *Dolichospermum* spp. (historically *Anabaena*) were reported in Lake Erie's western basin in the early 1900′s as nutrient loads to Lake Erie increased (Allinger and Reavie, 2013; Davis, 1954; Steffen et al., 2014; Watson et al., 2016). Yet, it was not until the 1950′s, when nitrogen-fixing *Dolichospermum* and *Aphanizomenon* spp. dominated blooms, that the lake received increased public attention (Davis, 1954, 1964; Huisman et al., 2018; Steffen et al., 2014). Increased nutrient inputs and resulting dense blooms shifted Lake Erie's trophic status from mesotrophic to hypereutrophic (McKindles et al., 2020; Sweeney, 1995; Verduin, 1964). This became a major impetus for the Great Lakes Water Quality Agreement (IJC, 1978), part of which targeted point sources of phosphorus to decrease algal blooms. This solution was successful for a time, and Lake Erie was pronounced "rejuvenated" (Sweeney, 1995) when cyanobacterial blooms decreased throughout the 1980's (Makarewicz and Bertram, 1991; Makarewicz et al., 1999; Nicholls and Hopkins, 1993). Yet, cyanobacterial blooms returned in the mid-1990's (although now dominated by non-nitrogen fixing *Microcystis* and *Planktothrix* spp.) coincident with the re-eutrophication of Lake Erie (Bridgeman et al., 2013; Brittain et al., 2000; Conroy and Culver, 2005; Watson et al., 2016). Since then, *Microcystis* spp. has been ecologically successful – routinely outcompeting various summer phytoplankton in the water column (Wilhelm et al., 2020). Blooms dominate the western basin nearly every summer incurring consequences for ecosystem and human health while capturing the attention of the popular press (Fig. 1) (Ames et al., 2019; Bridgeman et al., 2013; Pound et al., 2022; Rinta-Kanto et al., 2009a; Steffen et al., 2017). While *Microcystis* spp. has proliferated throughout the western basin of Lake Erie, this lake is far from a monoculture. Until recently, *Planktothrix* spp. dominated Sandusky Bay (McKindles et al., 2021; McKindles et al., 2022; Rinta-Kanto and Wilhelm, 2006) while

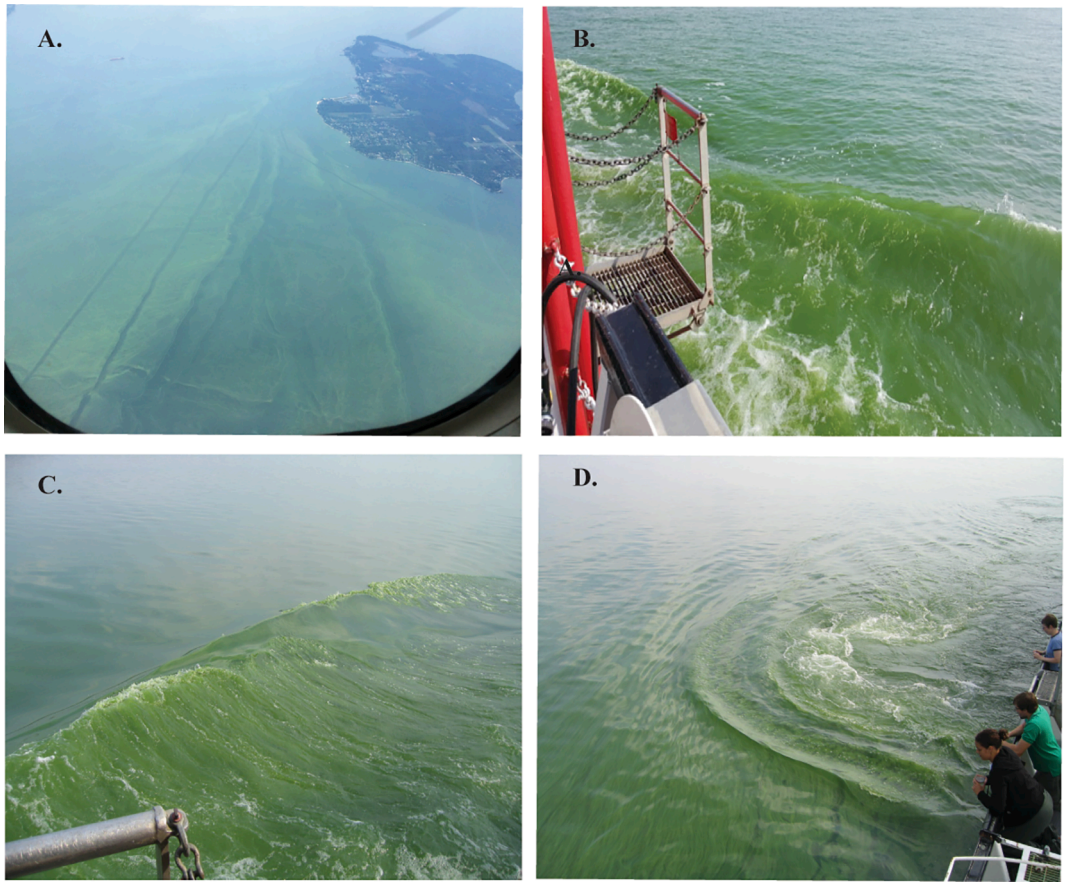

Fig. 1. Summer cyanobacterial blooms (mainly comprised of *Microcystis* spp.) throughout the Lake Erie western basin spanning summer 2003–2023. (A) Aerial view of a large cyanobacterial bloom within the western basin of Lake Erie. (B-D) Images of green-colored wake due to the prolific biomass of cyanobacteria and the formation of cyanobacterial surface scums. Photo credit: Steven W. Wilhelm.

Box 1
Defining a "bloom".

This question has been a topic of debate for decades (Smayda, 1997). In a review of the literature, using *Microcystis* spp. as a case study, we found the following definitions:

1) The visible formation of scum or discoloration (Huisman et al., 2018; Kalff, 2002; Reinl et al., 2021; Reinl et al., 2023).

2) Elevated Chl *a* concentration - due to phytoplankton - indicating eutrophic (range 3-78 mg m^{-3}) or hypereutrophic (100-150 mg m^{-3}) conditions (Wetzel, 2001).

3) An elevated fluorescent signature of photopigments (phycocyanin and/or Chl *a*) detected *via* satellite imagery (Hou et al., 2022; Vincent et al., 2004; Wynne et al., 2010).

4) A combination of elevated algal pigment concentrations coinciding with cyanotoxins (Berry et al., 2017; Qian et al., 2021).

5) A perceivably large contribution to total phytoplankton biovolume calculated *via* cell counts/microscopy (Reavie et al., 2014; Reavie et al., 2016).

6) Dominance of a genus in sequencing data (Pound et al., 2022; Rinta-Kanto et al., 2005; Steffen et al., 2017).

Overall, there remains no objective and universal metric to qualify a bloom and researchers rarely define what they consider a bloom in publications. To this end - and for the purpose of this paper - we offer a definition to clarify the question "what is a bloom?":

An algal bloom is a symptom of an unbalanced ecosystem caused by the unconstrained growth of a single algal group (or a few genera) which results in elevated pigment concentration, biovolumes and/or cell abundances > 5% of the historical median. This dominance (>55%) of one or a few genera alters baseline water column physiochemistry and ecosystem function.

Dolichospermum and *Aphanizomenon* spp. routinely manifested in the western-central basins (Chaffin et al., 2019; Wynne and Stumpf, 2015; Yancey et al., 2023b). Furthermore, within each cyanobacterial bloom-forming species there are numerous strains and genotypes, introducing further diversity within community composition, fitness and response (Li et al., 2016; Liu et al., 2014; Matson et al., 2020; McKindles et al., 2022; Sheik et al., 2022; Yancey et al., 2023a). Nonetheless, the ecological success of summer cyanobacterial biomass is attributed to nutrient (Paerl et al., 2016) and temperature paradigms (Huisman et al., 2018; Paerl and Huisman, 2008), with climate change exacerbating blooms across the aquatic continuum (Wells et al., 2020; Zepernick et al., 2023).

In contrast to their summer success, some cyanobacteria (such as *Microcystis* spp.) were thought to remain quiescent within the sediment throughout the winter-spring period (Rinta-Kanto et al., 2009b) though additional surveys are needed (Powers and Hampton, 2016). Yet, other cyanobacteria are routinely abundant in winter months: genera such as *Synechococcus* and *Cyanobium* spp. are examples of the abundant pico-cyanobacteria that are components of winter and summer Lake Erie planktonic communities (Wilhelm et al., 2014). These genera contribute to algal biomass (Carrick and Schelske, 1997; Fahnenstiel and Carrick, 1992) and routinely reach concentrations exceeding 100,000 cells L^{-1} in both summer (Ivanikova et al., 2008; Wilhelm et al., 2006) and winter periods (Twiss et al., 2012). While these species are persistent, they are often overlooked in assessments of the cyanobacterial community in Lake Erie, though the importance of these picoplankton has been described in estuarine studies (Gaulke et al., 2010; Paerl et al., 2020) and other lakes (Paerl, 1977; Stockner and Antia, 1986). Given the potential for this size-fraction to contribute notably (*i.e.,* 17–37%) to water column chlorophyll (Carrick and Schelske, 1997; Ivanikova et al., 2008), it is clear that assessment of these genera needs to be included to fully understand ecosystem processes. More broadly, the potential presence of cyanobacteria within the winter-spring water column requires attention across freshwater systems.

Ecological success of Lake Erie diatoms

While diatoms have had episodic recognition of high abundances within the literature (Stoermer et al., 1996; Stoermer et al., 1993), they lack the notoriety given to cyanobacteria. For example, a Web of Science search of all articles describing "Lake Erie cyanobacteria blooms" resulted in 235 article results since 1990 whereas "Lake Erie diatom blooms" only resulted in 30 (search performed May 2023). This can be attributed to the fact that Lake Erie diatoms are not known to produce toxins and thus are not a perceived threat to human health. That said, diatoms are not without ecological consequence (Reavie et al., 2016). According to the paleolimnological record, diatoms consistent with oligotrophic conditions (*Aulacoseira distans* and *Cocconeis disculus)* dominated the Lake Erie water column along with eutrophic-associated diatoms (*Stephanodiscus* spp., *Aulacoseira granulata*, *Cyclotella bodanica*) prior to 1850 (Sgro and Reavie, 2018; Stoermer et al., 1987; Stoermer et al., 1996; Stoermer et al., 1989; Stoermer et al., 1993). Subsequent nutrient loading throughout the first half of the twentieth century led to a regime shift within the diatom community, resulting in dominance by taxa such as *Fragilaria* and *Stephanodiscus* spp. in the eutrophied western basin (Britt, 1955; Hohn, 1969; Verduin, 1964). In turn, while diatoms largely dominated the Lake Erie summer water column for the first half of the twentieth century (Nicholls et al., 1977; Region and Davis, 1958), total diatom summer abundance declined into the 1960's (Britt, 1955; Casper, 1965). Yet, there remains a forgotten exception to this trend; prolific summer *Fragilaria crotonensis* blooms have been reported across the western basin of Lake Erie throughout the late 1960's and into the early 2000's (coinciding with the rejuvenation of Lake Erie), with concentrations of this chain-forming diatom reported as high as 950,000 filaments L^{-1} (Beeton, 1965; Gladish and Munawar, 1980; Hartig, 1987; Munawar et al., 2008; Munawar and Munawar, 1976). To date, this genus remains a prominent member of the Lake Erie summer water column (Bramburger and Reavie, 2016; Chaffin et al., 2019; Reavie et al., 2014; Saxton et al., 2012), though studies concerning its ecological success are limited (Hartig, 1987; Hartig and Wallen, 1986; Zepernick et al., 2021; Zepernick et al., 2022b). Cumulatively, the data indicate populations of diatoms are routinely abundant in the summer water column of Lake Erie regardless of shifts in trophic status and nutrient availability, yet these diatoms receive little recognition.

Beyond the historical summer diatom blooms, there are prominent winter-spring diatom blooms within Lake Erie (Beall et al., 2016; Edgar et al., 2016; Saxton et al., 2012; Twiss et al., 2012). Diatoms (including *Asterionella, Synedra, Stephanodiscus*, and *Cyclotella* spp.) were reported under Lake Erie's ice cover in the 1940′s throughout the western basin (Chandler, 1940; Chandler, 1942, 1944; Chandler and Weeks, 1945), and while their presence was occasionally acknowledged (Munawar and Munawar, 1982; Stoermer, 1975), they remained largely unstudied until recently. Dense blooms of the eutrophic diatoms *Aulacoseira islandica* and *Stephanodiscus binderanus* were rediscovered within and underneath Lake Erie ice cover by Twiss et al. (2012) (Fig. 2) across the western-central basins. Subsequent studies determined these diatoms were metabolically active, with Chl *a* concentrations and biovolumes that rivaled summer cyanobacterial blooms (Reavie et al., 2016; Saxton et al., 2012; Twiss et al., 2012). Yet, these same studies also demonstrated the winter diatom community has significantly changed since foundational surveys of winter communities (Chandler, 1940; Chandler, 1942, 1944; Chandler and Weeks, 1945), possibly due to contributions from eutrophication or the dreissenid mussel invasion. In addition, contributions to this community shift made by changes in nutrient loading and climate remain poorly understood to date. In summary, it seems clear from the gaps in knowledge outlined above that further studies concerning Lake Erie diatom characterization and ecophysiology would greatly benefit the broader limnological community.

What is a bloom?

Recent literature has indicated a need to revisit the age-old question "what *is* a bloom?" (Smayda, 1997). To investigate this question, we reviewed the literature using Lake Erie *Microcystis* spp. blooms as a case study to explore how others have previously defined a bloom. This literature review demonstrated a lack of consensus when it comes to defining a bloom, with different metrics and definitions employed over decades (Box 1). This of course creates confusion in both the discussion and execution of research. For example, it is broadly accepted that many researchers to this day employ the "bloom-chasing" technique: exploring an environment until a perceivable discoloration or surface scum is encountered in the water column then taking subsequent measurements (Qian et al., 2021). When a bloom is noted without a quantitative metric to reinforce the definition (*i.e.,* cell abundance, Chl *a* concentration, *etc.*), it is difficult to ascertain if the observations truly merit a "bloom". In turn, many of the metrics historically used to define a bloom (notably Chl *a*) are generalized and gloss over critical details. For example, elevated Chl *a* concentrations can be an initial means to detect a bloom, but without confirmation (*e.g.,* cell counts or other means) demonstrating that one genera (or a few) is truly dominating the photosynthetic community, is it really a bloom? In turn, how do we set a quantitative threshold for "domination" in a community? We appreciate establishing these metrics is challenging, yet it can be done as evidenced within the marine literature. For example, modelers within the marine field have developed fine-scale statistical cut-offs for what they consider to be a bloom, such as using 5% above annual median values of surface Chl *a* to define initiation times for bloom events (Henson and Thomas, 2007; Siegel et al., 2002) or a variety of statistical cut-offs pertaining to long term historical trends in Chl *a* data (Kim et al., 2009; McGowan et al., 2017). Yet, the freshwater field has been slow to establish such quantitative definitions. We offer a formal definition of an algal bloom in efforts to reconcile historical ambiguity (Box 1) and present ten key considerations when defining a bloom in a peer-reviewed study.

Key bloom considerations: 1) Formal definition: A definitive

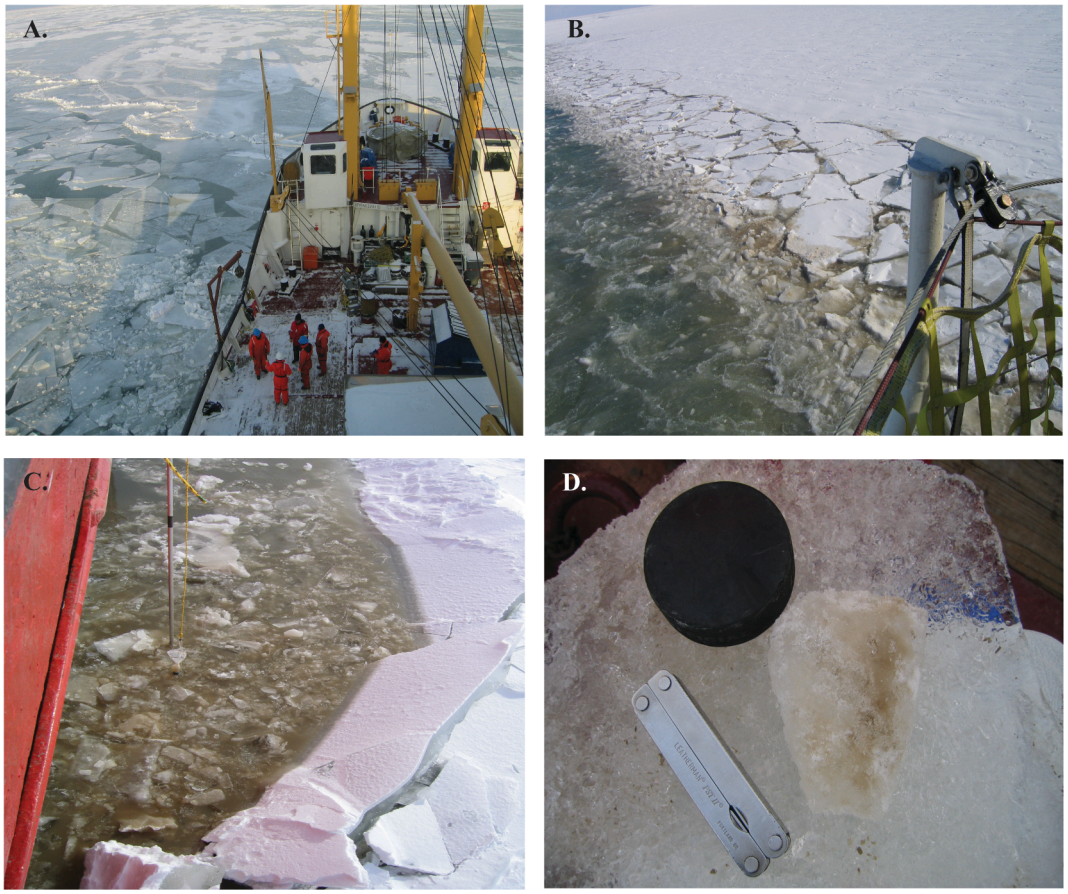

Fig. 2. Winter diatom blooms (mainly comprised of *Aulacoseira islandica* and *Stephanodiscus* spp.) throughout the Lake Erie western and central basins spanning winter 2007–2010. (A) Winter diatom blooms are difficult to access and oftentimes require an ice cutter. (B, C) Winter diatom blooms were initially thought to be "sediment plumes" due to their brown coloration and extensive biomass. (D) Certain diatoms such as psychrophilic *Aulacoseira islandica* and *Stephanodiscus* spp. embed within the surface ice cover. Photo credit: Steven W. Wilhelm.

statement of what authors are considering a bloom (and the metrics used to conclude this) should be included within manuscripts, allowing the reader to decide for themselves. 2) Chlorophyll requires clarification: Chlorophyll (μg L^{-1}, RFU, *etc*.) should be used as a first means to indicate the community is "unbalanced" and exhibiting eutrophic or hypertrophic symptoms. We suggest rather than a universal cut-off for trophic status, this number should be based on historical chlorophyll data pertaining to the system of study and suggest using 5% above annual median values of surface Chl *a* to define bloom status in accordance with marine modelling literature. 3) Bloom *vs.* baseline: Establish species-specific abundance thresholds for what constitutes as a "bloom" of the genus as opposed to a baseline ecologically observed abundance. In turn, references to invaluable long-term monitoring datasets or prior publications should be included to leverage this (if available). 4) Demonstrate group/genus dominance: the bloom-forming group (*e.g.*, Cyanobacteria) and/or genus (*e.g.*, *Microcystis* spp.) that is the dominant member of the community should be quantified with cell counts *etc*. Here, we suggest 55% of the total phytoplankton community cell abundance (or comparable metric of assessment) is a suitable metric to distinguish dominance. 5) Persisting *vs*. Thriving: Efforts to demonstrate the bloom community is truly metabolically active should be performed (if feasible). This can include photosynthetic rates, nutrient uptake, growth dynamics, or specific viability indicators (*e.g.*, silicon deposition in diatoms). 6) Bloom duration and stage: Acknowledgment of the longevity of the bloom should be made (if feasible). For example, was this a bloom that has been present in the system for weeks based on satellite data or was it an episodic ephemeral event? In turn, noting the approximate stage of the bloom (initiation, peak, maintenance, termination) is recommended if possible. Studies have already demonstrated that these stages come with unique physiologies in *Microcystis* spp. blooms (Tang et al., 2018). 7) Vertical distribution of the bloom: the distribution of the bloom in the epilimnion should be noted if feasible, along with the time of day given many bloom-forming genera vertically migrate. 8) Ecosystem change: Action should be made to demonstrate the bloom is altering the normal physiochemistry of the water column by measuring turbidity, dissolved oxygen, pH, *etc*. 9) Beware of biovolume: When determining genus-specific bloom metrics, the bias of cell concentration *vs.* biovolume must be considered. For example, the biovolume of a *Microcystis aeruginosa* cell is substantially smaller compared to a chain-forming diatom filament such as *Fragilaria crotonensis*. 10) Supportive evidence: We note these metrics are not universally feasible (especially concerning programs with limited funding or field sites in remote regions, *etc.*). In turn, requiring all the aforementioned metrics in the report of a bloom would be incredulous and cumbersome. Rather, we propose these considerations serve as an ideal, feasible array of quantitative metrics one can choose from to define a bloom moving forward. In cases where means may be limited, efforts should be made to characterize the bloom with available resources (*e.g.,* turbidity measurements with a Secchi disk, images of the bloom, *etc.*).

In efforts to test our bloom definition and considerations, we applied them to phytoplankton relative abundance data (reported in contribution to total biovolume) across the western and central basin of Lake Erie (2010–2019) (Figs. 3, 4). Notably, this dataset used biovolume as the metric of assessment and thus we investigated the potential dominance of one group (>55% of the total community) and the magnitude of the total photosynthetic community compared to the long-term median

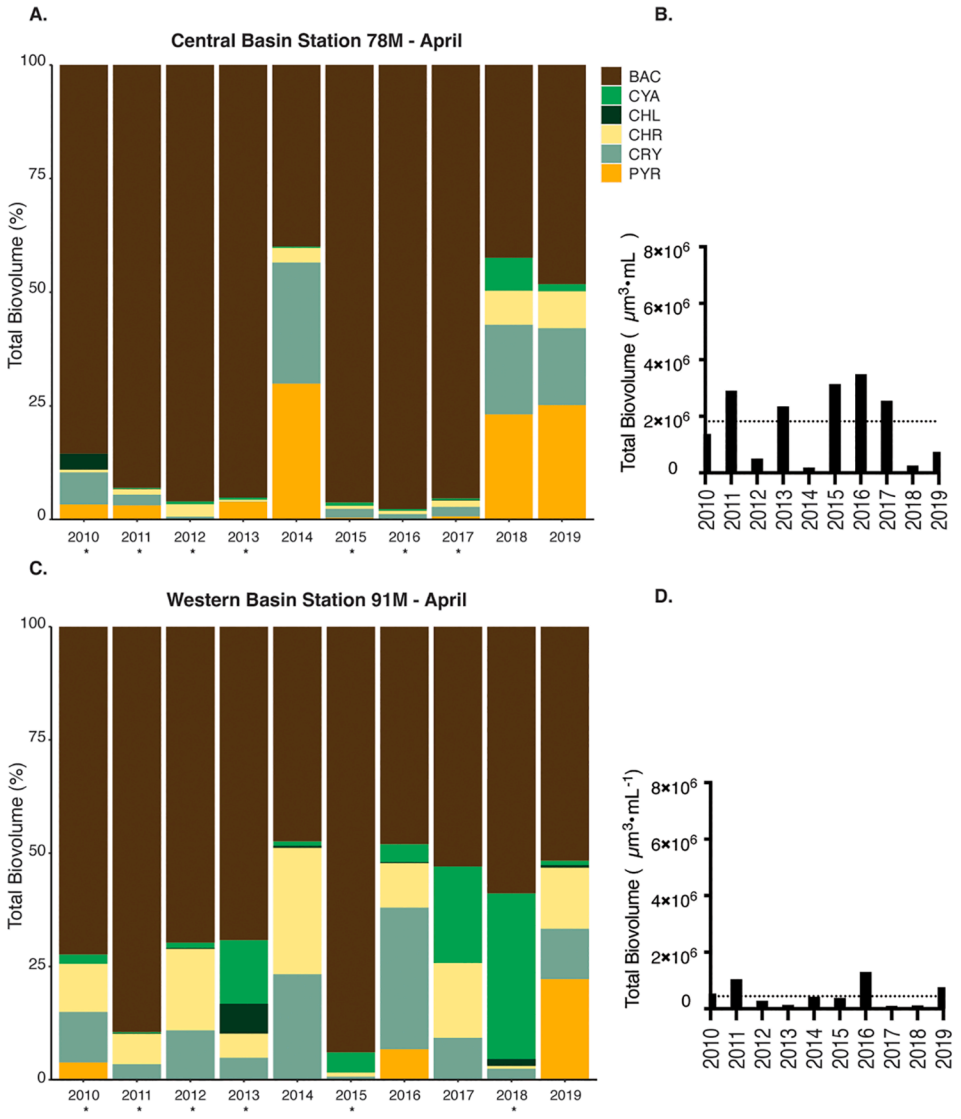

Fig. 3. Relative abundance of major phytoplankton taxa (reported as contribution to total biovolume) across the western and central basin throughout April 2010–2019. (A) Contribution of identified phytoplankton groups BAC = Bacillariophyta, CYA = Cyanobacteria, CHL = Chlorophytes, CHR = Chrysophytes, CRY = Cryptophytes, PYR = Pyrrhophytes to the total biovolume of these groups in the central basin of Lake Erie (U.S. EPA station 78 M) in the month of April. An asterisk indicates the community was dominated (>55%) by one group. (B) The total biovolume of the 6 main phytoplankton groups identified during the April 2010–2019 surveys at central basin station 78 M. Median total biovolume is indicated with a dotted line. (C) Contribution of identified phytoplankton groups to total biovolume of these groups in the western basin of Lake Erie (U.S. EPA station 91 M) during the month of April. (D) The total biovolume of the 6 main phytoplankton groups identified during the April 2010–2019 surveys at the western basin station 91 M. The water column temperature during April surveys ranged from 4 to 8° C. Data is publicly available through the U.S. EPA Great Lakes National Program Office (https://cdx.epa.gov/).

(>5% above the median seasonal total abundance from 2010 to 2019). Based on the available data, this exercise emphasized three points: 1) To be defined as a bloom the community must be dominated by a single group *and* exhibit overall biovolume or abundances higher the long-term median. For example, the photosynthetic community can be dominated by a single group (>55% diatoms) yet the total biovolume can be lower than the long-term annual median for that region suggesting these may not constitute as true blooms (*i.e.*, central basin station 78 M April 2010, 2012). In contrast, the total biovolume can be higher than the long-term median for that region yet there is a lack of dominance of any one group in the community, suggesting these may not be blooms (*i.e.,* central basin station 78 M August 2016). By applying just two of the bloom metrics from our list of 10 to historical data – we can assume that out of the 21 instances when the community was dominated by one group, only 10 were a "bloom" exhibiting elevated biovolumes above the long-term median and dominance by one group. 2) Opportunistic samples taken without temporal context can introduce bias and uncertainty. For example, our bloom definition does not qualify the cyanobacterial bloom of 2015 as a true "bloom" given the total biovolume was not > 5% higher than the long-term median. Yet, prior accounts suggest this was a bloom of large magnitude (Chaffin et al., 2018). Indeed, further investigation revealed this is a case where timing was of the essence. Our dataset (EPA, 2021) only sampled this area once a month over the course of years; in 2015 they sampled on August 11th (when the daily mean Chl *a* was ~ 42.69 $\mu g\ L^{-1}$ according to data from Chaffin et al. (2018)). In contrast, Chaffin sampled repeatedly throughout the entire summer season capturing the entire bloom including the bloom peak where Chl *a* > 100 $\mu g\ L^{-1}$ (July 28th-August 3rd) (Chaffin et al., 2018) (highlighting again the importance of sample design and repetition). Hence, according to Chaffin et al. (2018) this was a large bloom > 100 $\mu g\ L^{-1}$ (July 28th-August 3rd), which exceeded the long term seasonal summer median Chl *a* concentration of 17.09 $\mu g\ L^{-1}$. Yet, according to the EPA, who sampled

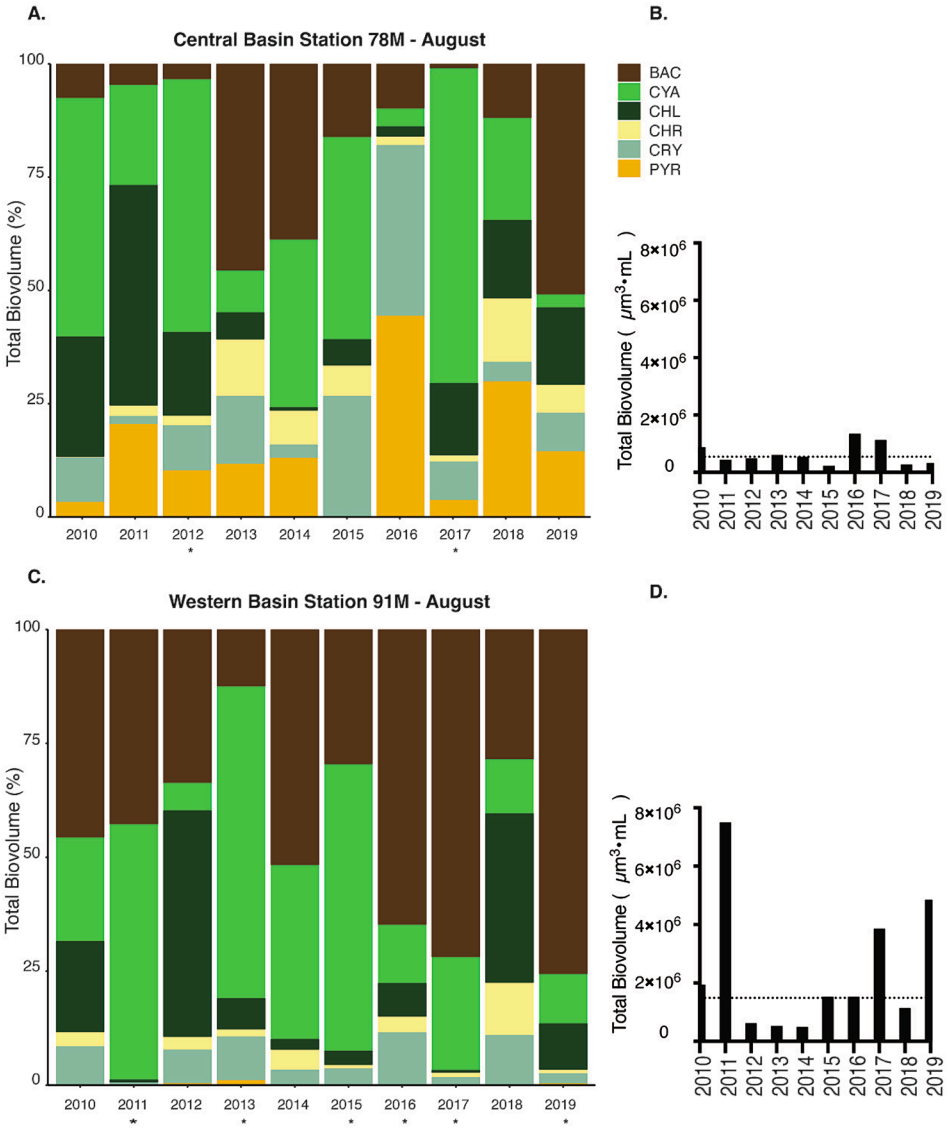

Fig. 4. Relative abundance of major phytoplankton taxa (reported as contribution to total biovolume) across the western and central basin throughout August 2010–2019. (A) Contribution of identified phytoplankton groups BAC = Bacillariophyta, CYA = Cyanobacteria, CHL = Chlorophytes, CHR = Chrysophytes, CRY = Cryptophytes, PYR = Pyrrhophytes to the total biovolume of these groups in the central basin of Lake Erie (U.S. EPA station 78 M) in the month of August. An asterisk indicates the community was dominated (>55%) by one group. (B) The net biovolume of the 6 main phytoplankton groups identified during the August 2010–2019 surveys at central basin station 78 M. Median total biovolume is indicated with a dotted line. (C) Contribution of identified phytoplankton groups to total biovolume of these groups in the western basin of Lake Erie (U.S. EPA station 91 M) during the month of August. (D) The net biovolume of the 6 main phytoplankton groups identified during the August 2010–2019 surveys at the western basin station 91 M. Data is publicly available through the U.S. EPA Great Lakes National Program Office (https://cdx.epa.gov/).

the following week after the bloom collapse, this was not a true "bloom" as the biovolume was not higher than the historical median. Thus, two studies of the same 2015 cyanobacterial bloom in the Erie western basin have drastically different conclusions despite sampling just a week apart. Indeed, this also applies to the large (and notorious) *Microcystis* spp. bloom of 2014. 3) Quantitative metrics have different implications. For example, in the comparison made between Chaffin et al., (2018) and the EPA, one study used Chl *a* as a metric to quantitatively assess the bloom whereas the other used biovolume. While each have their own strengths and merit, caution is needed when interpreting and comparing this data. For example, the biovolume of a diatom filament such as *Fragilaria crotonensis* is substantially larger than a single *Microcystis aeruginosa* cell – thus a smaller concentration of diatoms may make a substantial contribution to the total biovolume. In turn, photopigment concentrations per filament (or cell) can vary drastically based on the health of the algae; thus at times lower Chl *a* concentration (or fluorescence) does not always translate to less cells. In conclusion, care must be given when considering the interpretation of different quantitative metrics to ensure these variables are not applied (or extrapolated) improperly. Here, we have made an attempt to offer a bloom definition, key metrics for consideration and a case study review of these metrics in the context of Lake Erie blooms.

A seasonal bloom cycle in Lake Erie

Cyanobacteria and diatoms are the most prominent Lake Erie bloom-forming taxa, and they co-exist in a successional cycle: winter-spring diatom blooms are followed by summer cyanobacterial blooms (Wilhelm et al., 2020). Beyond this temporal separation of blooms, a spatial separation exists: cyanobacterial blooms largely dominate the western basin (Bridgeman et al., 2013; Jankowiak et al., 2019; Millie et al., 2009) while diatom blooms generally manifest in the central basin (Reavie et al., 2016; Twiss et al., 2012). Historically, this spatiotemporal

separation has led researchers to investigate these two blooms as separate, solitary events - focusing on one bloom organism (Hartig, 1987; Rinta-Kanto et al., 2009a) or one season (Millie et al., 2009; Twiss et al., 2012). We now know seasonal separation does not negate interlinkages between bloom events, rather the activity of one bloom sets the stage for the next *via* carbon accumulation, nutrient depletion, pH manipulation, *etc.* (Chaffin et al., 2018; Wilhelm et al., 2020; Zepernick et al., 2021). Yet, their spatial separation across lake basins has remained a confounding challenge to this precept. To address this, we performed a search within the historical Lake Erie data, and while this spatial generalization concerning large bloom events generally holds true, it is not always consistent. Seasonal phytoplankton data from stations in the western and central basins (2010–2019) (EPA, 2021) demonstrate diatoms dominated the phytoplankton biovolume during the spring throughout the western and central basins (Figure 3), but surprisingly met and often exceeded cyanobacterial biovolumes in summer within the western basin (Figure 4). Thus, this concept of spatially separated diatom and cyanobacterial blooms may not be as pertinent as previously thought. Beyond Lake Erie, we note this interlinked cycle is historically well-described in smaller lakes across the globe including Lake Constance (Germany) (Sommer, 1985), Mendota (US) (Stauffer, 1986), Erken (Sweden) (Yang et al., 2016) and Stechlin (Germany) (Padisák et al., 2004). Broadly, this successional cycle of taxa represents a well-known paradigm: the PEG (Plankton Ecology Group) model predicts that in productive freshwater systems the succession of the phytoplankton community proceeds from spring diatom blooms to early summer green algal and cryptophyte dominance, to large diatom dominance mid-summer, followed by cyanobacterial dominance late summer (Sommer et al., 2012; Sommer et al., 1986). This pattern is widely observed in eutrophic freshwater systems of various scales and sizes such as Lake Tai (China) and the English Windermere South Basin, among others (Canale and Vogel, 1974; Galat and Verdin, 1989; Goldenberg and Lehman, 2012; Ke et al., 2008; Krivtsov et al., 2000; Sitoki et al., 2012; Talling, 1976). In recent support, it was found winter-spring diatom bloom communities (and ice cover conditions) correlate with succeeding summer cyanobacterial dynamics in Petit-lac-Saint-François (Quebec, Canada) (Julian et al., 2024). Moving forward, much of the unexplained variation that is frequently observed in algal bloom studies may be attributed to the intrinsically linked nature of these events (Leflaive and Ten-Hage, 2007; Niu et al., 2011; Reavie et al., 2016).

3. Do physiochemical shifts in lakes column merit shifts in paradigms?

Freshwater systems across the globe are experiencing unprecedented change (Catalan et al., 2013; Gronewold et al., 2013; Gronewold and Stow, 2014; Huang et al., 2022; Oleksy et al., 2020). In tandem, cyanobacterial blooms are increasing in global distribution, duration, and frequency (Favot et al., 2019; Wells et al., 2020; Zepernick et al., 2023). Recently, this emergence of cyanobacterial blooms in historically "unusual" environments (*i.e.,* cold or oligotrophic) has been interpreted as a shift in classical paradigms thought to constrain bloom distribution (Reinl et al., 2021; Reinl et al., 2023). In contrast, we posit global change in lake physiochemistry has expanded the ecological niche of cyanobacteria – facilitating their emergence in novel environments now subject to the "old" paradigms. Here, we present this physiochemical change as two categories: 1) Long-term climatic shifts defined as large scale change from previous conditions which result in a "new normal" and 2) Short-term episodic disruptions defined as localized shifts from baseline conditions followed by a return to normal conditions. For example, long-term climatic shifts manifest as the warming of lakes and exacerbation of nutrient loading across the globe, both which serve to increase the prevalence of cyanobacterial blooms on a recurring basis. In contrast, episodic climatic extremes (droughts and floods) are intensifying due to climate change (Rodell and Li, 2023; Rohde, 2023) thus spurring ephemeral blooms. Increases in these episodic disruptions are culpable in the emergence of cyanobacterial blooms in previously unaffected systems by increasing nutrient loads during floods (episodic eutrophication) or by warming during droughts (thus stratifying the water column and concentrating nutrients), all of which prove favorable for cyanobacteria according to traditional paradigms (Paerl and Huisman, 2008; Paerl et al., 2016; Zepernick et al., 2023). In summary, both long-term climatic shifts and episodic climatic-driven disruptions are drivers of the physiochemical change (fluctuation in water level, temperature, dissolved nutrients, carbon dioxide (CO_2) availability, stratification, lake mixing *etc.*) responsible for this encroachment of cyanobacterial blooms within "novel" environments. An alternative way to phrase this is cyanobacterial blooms are not emerging in cold or oligotrophic environments, but rather traditionally cold environments are warmer and historically oligotrophic systems are eutrophied. Subsequently, we investigated examples of physiochemical change coinciding with bloom events that allegedly "shifted" paradigms in both the Great Lakes and smaller freshwater systems.

Revisiting the temperature paradigm

There exists a widely recognized paradigm for algal succession: cyanobacteria are adapted to warm, summer temperatures while diatoms thrive under cooler, winter temperatures. Indeed, studies have demonstrated cyanobacteria have relatively higher growth at elevated temperatures (Joehnk et al., 2008; Lürling et al., 2013; Reynolds, 2006; Robarts and Zohary, 1987). In addition, temperature alters water column structure: temperature-dependent density alters stratification while differing gas solubility can shape CO_2 availability (Wetzel, 2001). *Microcystis* spp. cells possess gas vesicles which allow them to benefit from temperature-induced stratification (Huisman et al., 2005; Paerl et al., 2006; Reynolds, 2006; Wagner and Adrian, 2009), contributing to an increase in cyanobacterial dominance of the water column (Kosten et al., 2012). Indeed, *Microcystis* spp. peak abundances coincide with high temperatures in Lake Erie (Davis et al., 2009; Rinta-Kanto et al., 2009a; Zepernick et al., 2021), lending strong support for the temperature paradigm. In turn, it has been previously suggested many cyanobacteria (such as *Microcystis* spp.) "disappear" or become numerically insignificant at temperatures $< 10^{\circ}$ C (Cao et al., 2022; Ming et al., 2022; Reavie et al., 2016; Visser et al., 2016). Yet, Reinl et al. (2023) recently cited 37 observations of freshwater cyanobacteria occurring at temperatures $< 15^{\circ}$ C across global freshwater systems, suggesting a need to revisit the school of thought that winter cyanobacteria are simply vegetative overwintering cells which are (at times) psychrotolerant rather than psychrophilic (Bridgeman and Penamon, 2010; Cirés et al., 2013; Kitchens et al., 2018; Kutovaya et al., 2012; Takamura et al., 1984). Specifically, Reinl et al. (2023) reported abundances of cyanobacteria which typically form summer blooms (*Dolichospermum, Aphanizomenon, Microcystis* spp.*)* in colder waters (Babanazarova et al., 2013; Bižić-Ionescu et al., 2014; Ma et al., 2016; Mankiewicz-Boczek et al., 2011; Persaud et al., 2015; Wejnerowski et al., 2018). While these reports may suggest a shift in the high-temperature paradigm, we offer an alternative interpretation: a closer look suggests many of these cyanobacterial blooms were caused by shifts in the physiochemical profile of the water column. For example, a cold *Microcystis* spp. bloom example included by Reinl et al. (2023) was reported in Lake Rupanco (Chile) (Fuentes et al., 2022). Yet, Fuentes et al. (2022) attributed this "unusual" bloom to shifts in physiochemistry (specifically increased nitrogen concentrations). In further support, "unusual" phytoplankton blooms have historically been attributed to shifts in physiochemical conditions (specifically warmer winters and large-scale climatic oscillations) in the well-studied Lake Constance (Germany) (Gaedke et al., 1998) and Lake Erken (Sweden) (Weyhenmeyer et al., 1999). Hence, while shifts in physiochemical profiles may increase the ability of cyanobacteria to tolerate cold temperatures or expand their realized ecological niche *via* warming / eutrophying events, the topic of whether they "like it cold" and are capable of thriving at these temperatures requires further inquiry.

As discussed earlier, Reinl et al. (2023) also noted a cold-temperature cyanobacterial bloom in Lake Erie, originally reported (but not as a bloom) by Twiss et al. (2012). However, historical data suggests this was not a bloom, but a routine abundance of an often overlooked picoplankton (Wilhelm et al., 2006). Nonetheless, the opinions expressed by Reinl and colleagues merit attention for Lake Erie and beyond. Cold tolerance in cyanobacteria is not a novel concept (Dietlicher, 1974; Los and Murata, 1999; Tang et al., 1997; Vincent, 2007), but it is seldom investigated. To investigate potential cold weather cyanobacterial events in our own records, we combed through data collected by the authors during 2018–2020 winter-spring Lake Erie surveys (Bullerjahn et al., 2022). We observed low concentrations of *Aphanizomenon* spp. (~128 cells L^{-1}) beneath ~ 45 cm of ice in February of 2019, and noted what might be considered relatively high concentrations of cyanobacteria (~1,800 cells L^{-1}) when water temperatures were ~ 10° C (Bullerjahn et al., 2022; Zepernick et al., 2022a). Yet, diatoms still dominated the water column during these periods. Further, McKay et al. (2018) reported *Planktothrix agardhii* concentrations > 1 x 10^7 cells L^{-1} during early May of 2016 in the Maumee River, a tributary of Lake Erie, when water temperatures were < 15° C. These cases raise the question if these were truly "blooms" and whether these populations were thriving under cold conditions or persisting due to regional shifts in the physiochemical water column.

Diatoms are also thought to be constrained by a long-standing temperature paradigm. Historically, the field has claimed diatom blooms are largely reserved to cold temperatures. Shatwell et al. (2008) embodied this paradigm by stating "It is well known that cyanobacteria prefer warmer temperatures than diatoms". While temperature does likely constrain particular Bacillariophyta ((*e.g.,* psychrophilic bloom-forming winter-spring diatoms) (D'souza, 2012; Jung et al., 2009; Saxton et al., 2012)), there exist prominent exceptions. Hartig (1987) reported prolific summer *Fragilaria crotonensis* blooms (~1 x 10^4 cells L^{-1}) throughout the western Lake Erie basin. These diatoms were proven to thrive at high temperatures by Hartig and Wallen (1986) who found *Fragilaria crotonensis* cultures (isolated from Lake Erie) reached maximum growth rates at 17–23° C compared to 5–11° C. In further support, recent studies with *Fragilaria crotonensis* demonstrated high growth rates at 26° C (Zepernick et al., 2021). Cumulatively, these studies suggest this diatom may be an exception to the temperature paradigm. If this is the case, it begs the question of why *Fragilaria crotonensis* blooms are not observed within the Lake Erie water column today? While warm temperatures can be optimal for growth of *Fragilaria crotonensis*, Hartig (1987) suggested they are constrained by 1) inadequate silica and phosphorus, 2) slight thermal stratification and wind, and 3) low turbidity. Notably, that study deduced a main driver of historic diatom pulses was "an order of magnitude increase in summer N:P ratios". Hence, while *Fragilaria crotonensis* does serve as an exception to the temperature paradigm, bloom events seem to only form when physiochemical conditions are ideal. It is worth noting there are a variety of diatoms abundant throughout the summer Lake Erie water column such as *Asterionella formosa*, *Synedra* spp. *Aulacoseira* spp., *etc.* (Reavie et al., 2014). Yet, there are few reports concerning summer diatom blooms (other than those by Hartig) in Lake Erie. Beyond the Great Lakes, Mancuso et al. (2021) reported diatoms, not cyanobacteria, were the dominant planktonic taxa throughout April-October in Muskegon Estuary (US), with summer temperatures at an average of ~ 23° C. Yet, this was an abnormally cold and wet summer, suggesting shifts in lake physiochemistry were responsible for this abnormal event. Another long-term monitoring study suggested climate-related variables such as warmer winters and variable ice cover have crucial effects on spring diatom dynamics in Saidenbach Reservoir (Germany) (Horn et al., 2011), noting these conditions can confound consequences of changing nutrient loads. In summary, while there is ample evidence to suggest diatoms can persist in the warmer water column, these populations appear to be hindered unless physiochemical conditions provide a competitive advantage. This area of research serves as a compelling opportunity: deducing what prevents diatoms from blooming may be as informative as deducing what triggers cyanobacteria to bloom. Broadly, Great Lakes diatoms still remain inadequately characterized (Edgar et al., 2016), with novel species discovered in Lake Erie as recently as 2023 (Reavie, 2023). Considering diatoms are under-characterized and numerically underestimated within Lake Erie, the evaluation of ecological paradigms amongst this taxon remains exceedingly difficult.

Revisiting the nutrient paradigm

An existing paradigm suggests cyanobacterial blooms are a symptom of eutrophication while diatoms are more commonly found in *meso*-oligotrophic systems. Anthropogenic nutrient loading is considered a primary driver of cyanobacterial blooms (Michalak et al., 2013). However, like the temperature paradigm, in the past few years the nutrient paradigm has been questioned. The notable emergence of cyanobacterial "blooms" within oligotrophic Lake Superior (US) was recently offered as evidence that may serve to "shift the high-nutrient paradigm" (Reinl et al., 2021). Yet, upon further investigation, these cyanobacterial pulses (comprised of *Dolichospermum* spp.) were hypothesized to be driven by physiochemical shifts manifesting as episodic increases in temperature and precipitation (resulting in eutrophication) (Sterner et al., 2020). Thus, again an alternative interpretation may exist: changes in physiochemistry are responsible for these ephemeral blooms as eutrophic conditions manifest in historically oligotrophic systems. Further, *Dolichospermum* and *Aphanizomenon* spp. are capable of nitrogen fixation which facilitates their persistence in oligotrophic systems (Willis et al., 2016). They also have relatively low temperature optima compared to *Microcystis* spp. (Paerl and Otten, 2016). Hence, this begs the question of whether ephemeral "blooms" of these genera truly shift the nutrient paradigm, or whether these genera are simply the most competitively fit to persist during temporary inputs of nutrients (episodic eutrophication events). Beyond Lake Superior, cyanobacterial blooms have been reported in oligotrophic freshwater systems in the U.S. (Murphy et al., 2023), Canada (Winter et al., 2011), and Europe. *Planktothrix rubescens* blooms have dominated Lake Hallwil (Switzerland) decades after its alleged re-oligotrophication (Suarez et al., 2023). Likewise, *Dolichospermum* spp. blooms have emerged in smaller subalpine (oligotrophic) Lake Maggiore (Italy/Switzerland) (Callieri et al., 2014). In addition, Favot et al. (2019) described "unprecedented" cyanobacterial blooms in a remote, oligotrophic Ontario lake (Canada), and concluded these blooms were due to physiochemical shifts in the water column. Indeed, these studies largely come to the same conclusions: physiochemical shifts are altering the nutrient loads within many of these systems, thus spurring cyanobacterial blooms (due to eutrophic conditions) in traditionally oligotrophic systems. Importantly, lake-wide trophic classifications are subject to caveats, as limnological partitions (epilimnion, metalimnion, or hypolimnion) within a body of water can contain vastly different levels of nutrients and thus constrain the distribution of algal taxa (Beaver et al., 2018). In considering this, physiochemical and climatic conditions within the lake again become a critical factor, as changes in temperature, wind patterns, and precipitation will alter the mixing of the water column and nutrient gradients, and thus the location of bloom-forming taxa. Cumulatively, this study suggests blooms in Lake Hallwil (and other oligotrophic systems) are largely due to shifts in the physiochemical profile of the water column, rather than shifts in the nutrient paradigm. In another example, the case of a cold-water cyanobacterial bloom in the oligotrophic waters of Lake Rupanco (Chile) becomes pertinent (Fuentes et al., 2022). These authors noted climatic changes shifted lake physiochemistry by elevating N:P ratios and increases in total nitrogen. More broadly, that study noted nitrogen contributions to the lake had increased in the past 36 years due to land use. Once again, physiochemical shifts coincided with the emergence of a cold-water cyanobacterial bloom, confounding the analysis of causation and whether this challenges paradigms.

Given the importance of diatoms to the algal bloom cycle, the nutrient paradigm with respect to diatom communities also deserves to

be re-assessed. While generally considered *meso*-oligotrophic species, in the preceding decades there have been various reports of diatom blooms in eutrophic freshwaters such as Lake Erie, Lake Michigan, Lake Victoria (Uganda, Kenya, Tanzania), and others (Hartig, 1987; Middelboe et al., 1995; Schelske, 1975; Sitoki et al., 2012). Most recently, *Asterionella formosa* blooms were reported in eutrophic Lake Tai (China), which is known for massive *Microcystis* spp. blooms (Liu et al., 2022). In addition, numerous diatom genera serve as eutrophic ecological indicators (Bellinger et al., 2006; Kitner and Poulícková, 2003; Vilmi et al., 2015). For example, increases in *Fragilaria crotonensis* and *Asterionella formosa* abundance have been used as indicators of nitrogen levels surpassing a trophic threshold in oligotrophic lakes throughout the western US (Saros et al., 2005; Spaulding et al., 2015; Wolfe et al., 2006). In addition, Stoermer (1993) indicated diatoms such as *Aulacoseira islandica, Fragilaria* and *Stephanodiscus* spp. serve as eutrophication indicators in the Lake Erie paleolimnological record. Yet again, due to the lack of studies concerning diatoms in these systems, conclusive interpretations remain difficult.

4. Do pH and light merit a role within algal bloom paradigms?

While temperature and nutrient availability are commonly described in successional studies, there remains considerable unexplained variation (Ke et al., 2008). This suggests additional factors constrain algal success and succession that remain unaccounted for in classical discussions. Here, we propose that pH and light availability merit renewed attention.

It is widely accepted pH constrains phytoplankton within the global oceans (Collins et al., 2014; Das and Mangwani, 2015; Gao et al., 2019; Lomas et al., 2012). Yet, compared to the abundance of marine pH studies, there is limited literature regarding the influence of pH on freshwater phytoplankton. This freshwater pH knowledge gap is of importance in the face of present and future climate scenarios. The Great Lakes are experiencing increases in pCO_2 (and thus declines in pH) coincident with the global oceans: it has been projected that water column pH in Lake Erie will decline by 0.3 – 0.4 units by 2100 (Phillips et al., 2015). Research suggests cyanobacteria exhibit higher growth rates on urea at alkaline pHs of > 7.7 (Belisle et al., 2016; Krausfeldt et al., 2019), thus they may be at a disadvantage at low pH levels. In contrast, acidifying surface waters may benefit diatoms (Arzet et al., 1986; Guillard and Lorenzen, 1972; Hervé et al., 2012), as a body of marine literature suggests diatoms prefer slightly acidic conditions (Bach and Taucher, 2019; Wu et al., 2014). Yet, in total there is a lack of information regarding how algae in Lake Erie will respond to low level, decadal increases in acidity. Acidity alters various phenomena, *e.g.*, nutrient speciation, CO_2 availability, trace metal solubility and microbiomes. These changes are likely to be significant for biology.

In contrast to atmospheric driven lake acidification across decades, biologically driven lake basification occurs on a diel and seasonal basis (Zepernick et al., 2021; Zepernick et al., 2022b). *Microcystis* spp. blooms (and other cyanobacterial genera (McGinn et al., 2003)) can increase the water column pH to $\sim$ 9.3 (Krausfeldt et al., 2019; Zepernick et al., 2021) by rapidly depleting CO_2 during photosynthesis (Badger and Price, 2003; Ji et al., 2020; Verspagen et al., 2014). This phenomenon has a broad footprint in the literature (Booker and Walsby, 1981; Klemer et al., 1982; Paerl and Ustach, 1982; Talling, 1976). Yet, few studies have directly assessed how cyanobacterial bloom-induced basification affects freshwater phytoplankton physiology. From the limited knowledge that exists, diatoms appear to be disadvantaged at elevated pHs. Alkaline pH conditions decrease growth rates and silica deposition in the Lake Erie model diatom *Fragilaria crotonensis* (*in vitro*) and environmental Lake Erie diatom communities (*in situ*) (Zepernick et al., 2021). Further, elevated pH levels were found to decrease the light-saturation thresholds of photosystem II and induce smaller, rougher, browner filaments in *Fragilaria crotonensis* (Zepernick et al., 2022b). Indeed, while diatoms are likely ecologically unsuccessful in the summer Lake Erie water column for a multitude of reasons (*i.e.*, slower growth rates, faster sinking rates, lack of gas vesicles, lack of extensive carbon concentrating mechanisms, *etc.*), pH appears to merit an addition to this list. On a broader scale, these studies imply a pivotal role of pH in algal bloom succession, as prolonged basification likely suppresses diatoms throughout the summer and delays fall diatom succession (Wilhelm et al., 2020; Zepernick et al., 2021; Zepernick et al., 2022b). In a cycle with profound implications, high pH may serve as a positive feedback mechanism for *Microcystis* spp. blooms (Krausfeldt et al., 2019; Shapiro, 1990; Tang et al., 2018) while serving as negative feedback (perhaps even a population control mechanism) for diatoms. Hence, there is a need to determine the effects of lake basification on the physiology of those inducing these events (cyanobacteria) and those otherwise affected (diatoms and other biota).

Beyond pH, studies have found novel implications of light availability within the success of seasonal blooms in Lake Erie (Beall et al., 2016; Chaffin et al., 2014; Edgar et al., 2016; Zepernick et al., 2024). It has been widely suggested light limitation shapes competition dynamics within the summer water column (Chaffin et al., 2014; Guildford et al., 2005; Jiang et al., 2015). Cyanobacterial scums frequently result in self-shading and the shading of underlying phytoplankton (Horst et al., 2014; Moore et al., 2017; Wu et al., 2021), increasing light attenuation and exerting pressure on other biota (*i.e.,* diatoms) within the water column and the benthos. Yet, direct assessment (and inclusion) of light climate and limitation with respect to summer Lake Erie communities remains largely unassessed, despite suggestions that seasonal light availability requires attention (Chaffin et al., 2014). In turn, recent evidence suggests a synergistic relationship between pH and light, as *Fragilaria crotonensis* filaments were found to exhibit reduced light saturation thresholds and phototolerance at elevated pH levels (Zepernick et al., 2022b).

In contrast to summer bloom-shading events, recent literature suggests light availability exerts selective pressures within the winter-spring water column (Beall et al., 2016; Zepernick et al., 2024). It has been shown in the absence of ice cover, wind-aided mixing resuspends sediment within the shallow isothermal water column of Lake Erie, resulting in turbid, light-limiting conditions (Chandler, 1944; Valipour et al., 2017). In further support, Beall et al. (2016) noted diatom abundances significantly declined in the turbid water column (2012) compared to the ice-covered water column (2011). They attributed this decline to light limitation based on photosynthetic parameters and mean light flux measurements in the water column. Most recently, Zepernick et al. (2024) revealed ice-free conditions exert selective pressure on the Lake Erie winter diatom community, selecting for taxa that possess certain adaptations (notably proton-pumping rhodopsins and fasciclins) which are thought to increase survival within the turbid water column. Cumulatively, these studies suggest climate change may not only incur temperature and pH effects, but also light.

5. Conclusion - *caveat biologus* (“let the biologist be wary”)

Biology is complicated, as is the ecology of algal blooms. Traditional concepts require revisiting and expansion in the face of new knowledge and rapid environmental change. Here, we re-visited key principals and paradigms used to explain harmful algal bloom success and succession employing Lake Erie as a case study.

We suggest diatom blooms merit inclusion in Lake Erie algal bloom discussions alongside cyanobacteria, noting diatoms are responsible for $\sim$ 20% of global primary production (Nelson et al., 1995), play an enhanced role in global biogeochemical cycles (Benoiston et al., 2017; Struyf et al., 2009) and represent a critical component of the aquatic ecosystem in global freshwater systems. Failure to include this critical lake constituent in bloom discussions represents a significant knowledge gap. Further, we propose Lake Erie winter-spring diatom blooms merit status as “harmful” algal blooms according to the standards set forth by Smayda (1997), noting the direct ecological consequence of these

blooms (large-scale hypoxia) (Reavie et al., 2016). Broadly, the freshwater field selectively (and subjectively) bestows the term "harmful" to algae which serve as a direct threat to human health due to their production of toxins (Bullerjahn et al., 2016; Ho and Michalak, 2015) while the marine field has acknowledged for decades algal blooms can be harmful based on anthropogenic threat (toxicity) and/or ecosystem health (Anderson, 2009; Anderson et al., 2008). In summary, revisitation of freshwater blooms and their "harmful" categorization requires attention, especially noting the direct effect this will have on policy, management and mitigation efforts.

More broadly, we must revisit what we define to be a harmful algal "bloom". Many have tried to tackle this term from the initial efforts to define a "bloom" by (Smayda, 1997) to more recent attempts to define what makes a bloom "harmful" (Ho and Michalak, 2015; Zingone and Enevoldsen, 2000). Yet, the consensus from these works has been simple. Scientists employ this term subjectively. Here, we offer a quantitative definition of a "bloom" in attempts to minimize ambiguity and offer key considerations to report when publishing a bloom study.

In addition, we provide support for a change in approach for algal bloom research. Due to the generalized spatiotemporal separation of diatom and cyanobacterial blooms in Lake Erie – these communities are often studied solitarily. However, we reviewed recent literature and historical data which suggest these blooms are intrinsically interlinked and should be studied in an integrative fashion which reflects the Lake Erie algal bloom cycle and more broadly the PEG model. The interdependent nature of the algal bloom successional cycle requires a comprehensive approach moving forward.

Contributing to our opinions in this piece is the presence of confounding factors which offer interpretations other than paradigm shifts. Indeed, while the discovery of cyanobacterial blooms in cold or oligotrophic freshwater systems can be interpreted as indication of shifts in paradigms, we provide an alternative interpretation and suggest this phenomenon is more likely attributed to the expansion of the cyanobacterial niche *via* climate warming and nutrient loading (*i.e.,* shifts in physiochemical conditions). Hence, we conclude the traditional ecological paradigms largely "hold-water". Yet, we recommend future bloom studies remain cognizant of the differences between the *acclimation* of freshwater communities to episodic events *vs. adaptation* to long-term change. In turn, bearing in mind the difference between a persisting and a thriving population will prove particularly pertinent, especially when exploring the potential of psychrophilic cyanobacteria. Beyond this, other observations and unexplained variation might be linked to "yet-to-be" accepted drivers of plankton community structure (*e.g.,* pH effects (Zepernick et al., 2021; Zepernick et al., 2022b) and light availability (Bramburger et al., 2023b; Zepernick et al., 2024)).

We note the conclusions derived from this case study of Lake Erie extrapolate beyond large-scale freshwater systems such as the Great Lakes (Baikal, Laurentian, African). These paradigms apply to smaller lakes across the globe, which are increasing in distribution and size (Downing, 2010), host a higher range of biodiversity (Bolgovics et al., 2019; Scheffer et al., 2006) and make a greater contribution to global carbon emissions compared to larger lakes (Pi et al., 2022; Zhou et al., 2022). Considering this, principles expressed within this manuscript become equally (if not increasingly) important in these systems. In addition, numerous long-term monitoring programs exist in smaller lakes which offer a unique opportunity to investigate the conclusions derived here (Kröger et al., 2023; Rhodes et al., 2017; Yang et al., 2016). Most recently, Lake Mendota (US) has been identified as a long-term water quality model (Hanson, 2023) and was recently used to forecast how legacy phosphorus and ecosystem memory constrain future water quality (Hanson et al., 2023). Moving forward, there is a need to interweave both smaller freshwater systems and the Great Lakes into future paradigm discussions.

Certainly, no one factor, or paradigm, is responsible for algal bloom success or succession at all times or in all places, and there exists ample evidence of the cross-effects and casual network of these paradigms in the literature. However, when paradigms are misinterpreted or incorrectly applied to biological phenomena, disconnects can occur between bloom events and bloom management (Bramburger et al., 2023a). For the limnologist, a return to many ecological principles (*e.g.,* competitive exclusion theory (Hardin, 1960)) is ripe for examination in the context of freshwaters. Often the devil is in the ecological details, and this cautionary tale must be kept in mind as the field increasingly relies on models to predict bloom magnitude and severity.

CRediT authorship contribution statement

BNZ writing - original draft. All author contributed to writing - reviewing and editing.

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.

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