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Review

Challenges in tracking harmful algal blooms: A synthesis of evidence from Lake Erie



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ABSTRACT

Harmful algal blooms (HABs) are becoming increasingly common in freshwater ecosystems globally, raising complex questions about the factors that influence their initiation and growth. These questions have increasingly been answered through mechanistic and stochastic modeling efforts that rely on historical information about HABs in a given system for development, validation, and calibration. Therefore, understanding processes that control HABs is predicated on the ability to answer much more basic questions about what has actually occurred in a given system, namely questions of HAB occurrence, extent, intensity, and timing. Here we explore the state of the science in answering these basic questions; we use Lake Erie as a case study, where nearly two decades after the resurgence of HABs, a summer 2014 event caused a mandatory three day tap water ban for Toledo, Ohio. We find that, even for well-studied systems, unambiguous answers to basic questions about HAB occurrence are lacking, raising concerns about their use as a basis for addressing mechanistic questions about controlling factors. This ambiguity is found to be caused by differences in the methods used to track HABs, the specific harm being considered, the linkage to that harm (direct or indirect), the threshold defining harm, and spatiotemporal variability in sampling. Further work is therefore needed to integrate heterogeneous types of observations in order to better leverage existing and future monitoring programs, and to guide modeling efforts toward deeper understanding of HAB causes and consequences.

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Introduction

Harmful algal blooms (HABs) in freshwater systems are quickly becoming a global epidemic. Reports of HABs in Lake Taihu in China (e.g., Qin et al., 2010), Lake Erie in North America (e.g., Michalak et al.,

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2013), Lake Victoria in Africa (e.g., Sitoki et al., 2012), and Lake Nieuwe Meer in The Netherlands (e.g., Johnk et al., 2008) constitute examples of an alarming trend in freshwater ecosystems worldwide that is only expected to worsen under a changing climate (Paerl and Huisman, 2009). The effects of HABs are well documented: they are associated with acute morbidity and mortality across a range of biota (including humans) (Landsberg, 2002; Van Dolah, 2005), economic impacts through ecological and human health costs (Anderson et al., 2000; Hoagland et al., 2002) and the need for additional water treatment measures for regions relying on surface water supplies (Hitzfeld et al.,

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2000; Hoeger et al., 2005). A HAB in Lake Erie during the summer of 2014 resulted in a three-day tap water ban for Toledo, Ohio (Wilson, 2014), providing an acute reminder of the impacts of HABs and the urgency of addressing their proliferation. The need for scientifically-guided policy to mitigate these impacts has never been greater.

The biogeochemical processes controlling the global increase in HABs are the topic of extensive ongoing research. Much of the debate has centered on HABs in marine ecosystems, and similar stressors apply in freshwater systems (Beeton, 2002). Four main hypotheses for the apparent increase have emerged: increased scientific awareness of toxic species, increased anthropogenic nutrient loading, increased frequency and magnitude of extreme climatic events, and increased exposure to invasive species (Hallegraeff, 2003). Understanding the role of each of these mechanisms in explaining global HAB trends is an ongoing area of research (Perovich et al., 2008).

Testing these hypotheses also involves answering questions about what causes a HAB to occur and what affects the timing, spatial extent and intensity of a HAB. Addressing these questions is a first step towards developing a predictive understanding of HAB dynamics, and therefore towards developing management strategies that limit HAB occurrence or growth. The growing effort to develop predictive mechanistic and statistical models for HABs (e.g., Walsh et al., 2001; Raine et al., 2010), and data-driven probabilistic models (e.g., Kang et al., 2011; Cha et al., 2014) relies heavily on existing data on HAB occurrence, spatial extent, and timing for model development, validation, and calibration. Using such models to answer fundamental questions about HABs is predicated, therefore, on the ability to answer much more basic questions about what has actually occurred in a given system. Chief among them:

- What is a HAB? (i.e., How do we identify blooms and whether or not they might be harmful?)
- Was there a HAB? (i.e., How do we define their occurrence?)
- How big was the HAB? (i.e., What are meaningful quantitative methods for establishing spatial extent?)
- When did the HAB occur? (i.e., When did a given HAB start, peak, and decline?)

Only when such questions are answered can a meaningful exploration of what is causing HABs begin.

We explore the state of the science in answering these seemingly basic questions through the lens of the literature available for Lake Erie, one of the Laurentian Great Lakes. Lake Erie provides a particularly appropriate test bed because it has been extensively studied over several decades, because conditions in recent years have conspired to produce some of the largest HABs ever observed in the lake (e.g. Michalak et al., 2013), and because these HABs have caused substantial harm including a mandatory tap water ban in Toledo, Ohio, in the summer of 2014. The severity of recent HABs has also led to the emergence of predictive modeling efforts in the literature (e.g., Stumpf et al., 2012; DePinto and Scavia, 2013; Obenour et al. 2014), making the need for evaluating the data used to support such efforts especially salient. To explore the questions outlined above, we present a synthesis of the evidence provided by published methods in establishing HAB occurrence, extent, intensity, and timing. We also explore whether, and to what degree, the diversity in available approaches impacts the answers to these basic questions, and implications for future monitoring and scientific inquiry.

Definitions: What is a HAB?

A *harmful* algal bloom is defined by its potential to harm humans and/or ecosystems, but defining harm has proven challenging. Earlier work has explored the criteria that algal species need to meet to be characterized as harmful, the abundance thresholds that define a HAB, and the diversity of pathways that can lead to the occurrence of a HAB of a particular species (Smayda, 1997; Zingone and Enevoldsen, 2000). Some groups have also made a distinction between "harmful" blooms as ones having health impacts and "nuisance" blooms as ones

that are linked to a more general class of harm (Watson and Boyer, 2013). The main conclusion from earlier analyses is that the definitions of HABs implied in the literature are subjective, stemming from differences in the harmful impacts being considered (Richardson, 1989; Smayda, 1997; Zingone and Enevoldsen, 2000).

We argue here that the question of what constitutes a HAB is more subtle still, by exploring a case where the target species is known and known to lead to at least some impacts that have been qualified as being harmful. In the case of Lake Erie, the primary species of concern is Microcystis aeruginosa, known for its secretion of the hepatotoxin microcystin and its use of buoyancy to out-compete other species (Steffen et al., 2014). Although other harmful species have also been observed in Lake Erie, e.g., Aphanizomenon spp., Anabaena spp., Cylindrospermopsis spp., and Planktothrix spp. (Allinger and Reavie, 2013; Conroy et al., 2007), Microcystis has been the dominant species in HABs at least since the mid-1990s (Brittain et al., 2000). HABs dominated by cyanobacteria (a.k.a. cHABs or cyanoHABs) such as Microcystis are especially relevant for study as they are rapidly proliferating globally (Paerl and Huisman, 2009). We explore how HABs have been defined through the lens of the metrics used in monitoring the lake, the types of harm considered, the nature of the linkage between metrics and harm (direct/indirect), and the degree to which that linkage is explicit. Note that here and in subsequent sections, we use the terms HAB and bloom interchangeably when discussing Lake Erie HABs.

The occurrence of blooms has been defined in Lake Erie using various types of metrics (Fig. 1 and Electronic Supplementary Material (ESM) Appendix S1). An in-depth review of the methodologies associated with these metrics and their advantages/disadvantages is available in Srivastava et al. (2013), and a timeline of studies making use of these metrics for Lake Erie is provided in ESM Table S1. Biomass and/or biovolume abundance has been reported in terms of total phytoplankton, total cyanobacteria, and/or individual species abundance (Bridgeman et al., 2013; Brittain et al., 2000; Conroy et al., 2005; Davis et al., 2012; DeBruyn et al., 2004; Dyble et al., 2008; Millie et al., 2009), and chlorophyll a (chl a) concentration has also been used as a proxy for total abundance (Becker et al., 2009; Conroy et al., 2005; Davis et al., 2012; DeBruyn et al., 2004; Millie et al., 2009; Ouellette et al., 2006; Rinta-Kanto et al., 2005). Microcystis-specific DNA analyses have been reported to confirm presence (Dyble et al., 2008; Ouellette et al., 2006; Rinta-Kanto et al., 2005; Rinta-Kanto and Wilhelm, 2006), and cell counts combined with the other metrics listed here have been used to quantify the relative abundance of *Microcystis* within the total cyanobacterial or phytoplankton population (Brittain et al., 2000; Conroy and Culver, 2005; Millie et al., 2009; Ouellette et al., 2006; Rinta-Kanto et al., 2009). Presence and concentrations of microcystin, a toxin secreted by some cyanobacteria including *Microcystis*, have been reported as a measure of the toxicity associated with blooms (Boyer, 2008; Brittain et al., 2000; Dyble et al., 2008; Millie et al., 2009; Rinta-Kanto et al., 2005; Rinta-Kanto et al., 2009) although the concentration of microcystin is not necessarily proportional to the amount of Microcystis. Remote sensing has also been invoked to identify blooms, based on different biotic and abiotic metrics that use algorithms to relate satellite reflectance data with in situ observations (Budd et al., 2002; Dash, 2005; Vincent et al., 2004; Becker et al., 2009; Wynne et al., 2010). More qualitative depictions of blooms use reports of surface scums appearing in the peer-reviewed literature, in news outlets, (e.g. "a thick slick of green paint" (Taylor, 1997)), in governmental reports ("surprising Microcystis blooms of 1998" (LaMP Work Group, 2002)), and in anecdotal reports ("reports of Microcystis by anglers" (Budd et al., 2002)). The presence of surface scum is dependent on in situ hydrodynamic conditions, however, and is therefore not a definitive identifier of HABs.

How these various metrics differ in their analytical approach and their applicability for regular monitoring is detailed elsewhere (Srivastava et al., 2013). For this discussion, we focus on how they differ in their relationship to harmful impacts. First, the metrics differ in the

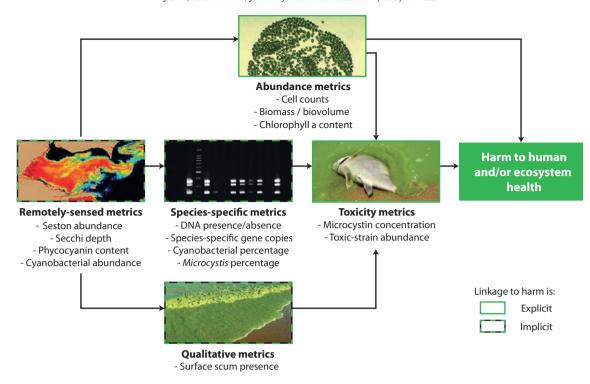


Fig. 1. Metrics reported in the literature for monitoring HABs in Lake Erie, categorized by their linkage to harm to human and/or ecosystem health, used here as one example of "harm" considered in the definition of HABs. Images provide examples of remotely-sensed cyanobacterial abundance (*Remotely-sensed metrics*, NOAA, 2011); DNA presence from a PCR gel image (*Species-specific metrics*, Rinta-Kanto et al., 2005); surface scum presence (*Qualitative metrics*, source: Tom Archer); microscopic *Microcystis* cell counts (*Abundance metrics*, source: Isao Inouye (University of Tsubaka), Mark Schneegurt (Wichita State University), and Cyanosite (www-cyanosite.bio.purdue.edu)); and fish mortality due to high microcystin concentration (*Toxicity metrics*, source: Tom Archer).

type of harm they best represent. For instance, microcystin is most closely linked to harm to human and/or ecosystem health via toxicity, whereas surface scum is most closely linked to harm to aesthetic quality and/or light availability. Second, the metrics differ in how directly they capture the link to the specific harm. For example, the link from remotely-sensed metrics to harm is indirect (Fig. 1), because the connection depends on how representative the captured information is of toxicity and/or aesthetic impairments. Similarly, qualitative metrics such as the presence of surface scum can be linked to higher toxin concentrations (Falconer et al., 1999) and therefore to harm to human and/or ecosystem health (Fig. 1). However, surface scum is not always associated with high toxin levels and therefore is only indirectly tied to that harmful impact. Third, the linkage between some types of metrics and harm is sometimes not made explicitly in specific studies, but rather implicitly. Explicit thresholds exist for relating some metrics to harm in the form of impacts on human health (e.g., Falconer et al., 1999), but this is not the case for each harm/metric combination. For instance, remotely-sensed phycocyanin is linked to harm to human health because phycocyanin is associated with cyanobacteria, and Microcystis has been the dominant cyanobacterial genus historically. As some strains of Microcystis are toxic, remotely-sensed phycocyanin has therefore implicitly been linked to potential harm to human and/or ecosystem health in some papers (e.g., Vincent et al., 2004). Indirect linkage to harm is often, but not always, associated with the linkage also being implicit rather than explicit (Fig. 1). Parsing out the assumptions underlying the use of a particular metric makes it possible to pinpoint the type of harm being considered, the directness of the linkage between the metric and the harm, and the explicitness of that linkage.

The diversity of metrics, harms, and types of linkages between the two suggests that what constitutes a HAB is therefore not straightforward, and as a result conclusions may not be immediately comparable

across studies using different metrics. The simple question "What is a HAB?" thus continues to be one that is subjective, even for systems such as Lake Erie where the primary species of interest is known.

Faced with this ambiguity, some groups have selected subsets of harms and metrics, as well as specific thresholds, to define HABs from an operational standpoint. The International Joint Commission (IJC; Watson and Boyer, 2013) and the Ohio Environmental Protection Agency (Ohio EPA; Kasich et al., 2014), for example, have defined HABs based on thresholds for microcystin, chl a, and cell concentrations. For microcystin, the World Health Organization (WHO) has defined 1 µg/L microcystin as the threshold for drinking water intended to be safe for life-long exposure (World Health Organization, 2004), and 10 µg/L (mild probability of health effects) and 20 µg/L (moderate probability of health effects) as the thresholds for recreational water use (World Health Organization, 2003). The two higher WHO thresholds have been adopted for monitoring pelagic and benthic sites by the IJC (Watson and Boyer, 2013), while the Ohio EPA has adopted the 1 µg/L and 20 µg/L thresholds for "Do not drink" and "Do not use," respectively (Kasich et al., 2014). Similarly, WHO has thresholds for *chl a* of 10 µg/L for increased odds of irritative or allergenic effects, and 50 µg/L for increased probability of irritative symptoms and toxic impacts, both under conditions of cyanobacterial dominance (Falconer et al., 1999). These thresholds are equivalent to cyanobacterial abundance thresholds of 20,000 and 100,000 cells/mL based on toxicological assumptions (Falconer et al., 1999). The IJC and Ohio EPA have selected chl a thresholds similar to the WHO range, namely a 30 µg/L threshold for IJC (Watson and Boyer, 2013), and 2, 5, and 50 µg/L (or 4,000, 10,000, and 100,000 cyanobacterial cells/mL) thresholds adopted by the Ohio EPA for minor, moderate, and severe blooms, respectively (Kasich et al., 2014). Beyond microcystin and chl a, the IJC has also adopted 80% biomass of harmful species as another threshold indicative of HABs (Watson and Boyer, 2013).

Although these thresholds have clarified what constitutes HABs for certain groups, the specific choices that had to be made, and the diversity among the definitions selected by the WHO, IJC, and Ohio EPA, further highlight that, although intelligent decisions as to operational definitions can be made, a single clear scientific definition is elusive. This diversity in metrics, harms, and forms of linkages between them can be problematic for addressing more complex questions if the choice of metrics leads to contradictory conclusions. For instance, if inferences based on measurements of *Microcystis* biovolume differ from those based on cyanobacterial biomass, then mechanistic models validated against one or the other metric could yield substantively different results. This is especially true if different metrics disagree on seemingly straightforward questions of bloom occurrence, extent, and timing. This topic is explored in the following sections.

Occurrence: Was there a HAB?

Assessing whether or not a HAB has occurred, specifically dichotomizing years into "bloom" and "non-bloom" years (where bloom here implicitly refers to HABs), has become an increasingly common way of understanding HABs in Lake Erie (Brittain et al., 2000; Davis et al., 2012; Dyble et al., 2008; Stumpf et al., 2012). In this framework, however, it would be problematic if different metrics, along with the thresholds for dichotomization associated with each, led to different prescriptions for a bloom having occurred, especially because such designations are often used to inform further analysis (e.g., Stumpf et al., 2012). In this section, we explore whether, and to what extent, such designations are sensitive to the methods used.

To answer this question, we synthesize evidence from the literature on bloom occurrence from 1995 to 2011 in Lake Erie (Fig. 2A; individual evidence from each study in ESM Table S2). The studies all report data collected between July and September, but range from reporting data collected on single days to data collected periodically at given intervals. Because blooms have peaked anywhere between July and September historically, it can be difficult to determine whether evidence reported by a specific study was collected at the right time to capture the occurrence of a HAB. As such, Fig. 2A reports all evidence as presented in the studies without consideration of when blooms peaked.

Each reported metric from a unique data set for a specific year is weighted as one piece of evidence. Evidence for bloom presence is determined based on whether the reported metric is above literature-reported thresholds for harm. We use 1 µg/L for microcystin (World Health Organization, 2004), 10 µg/L for chlorophyll a (World Health Organization, 2003) and 20,000 for cyanobacteria cells/mL (Falconer et al., 1999), corresponding to the standards used by the most conservative peer-reviewed studies that report these metrics (i.e., Brittain et al., 2000; Millie et al., 2009; Dyble et al., 2008, respectively). We note that these thresholds used in the literature are more conservative than the IJC thresholds and less conservative than those from the Ohio EPA. For metrics with no published thresholds, the reported metric is assessed based on its magnitude relative to other years in multi-year studies, or interpreted as such based on the original study authors' determination (full methodology in ESM Appendix S1).

In Lake Erie, HAB presence is usually assessed on an annual basis, with blooms typically occurring in late summer after the spring precipitation brings nutrients into the lake. Fig. 2A shows which years in this period have mostly consensus evidence for bloom presence (95, 98, 03, 08–11) or absence (96–97, 07), and which years have mixed evidence (99–02, 04–06). In the years where there is consensus, cyanobacteria are typically either close to completely absent (e.g., 1996) or relatively abundant (e.g., 2011), resulting in measurements either far below or far above the thresholds for harm. Of the years with mixed evidence, however, measurements near the "bloom" thresholds shed insight on distinctions between methods. In particular, 2002 and 2004 highlight important distinctions in the results from different metrics.

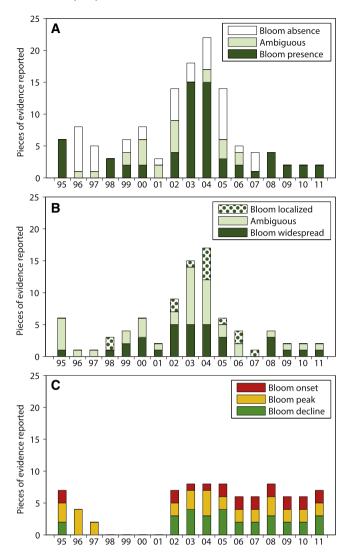


Fig. 2. Evidence on bloom (A) occurrence, (B) size and (C) timing for studies on Lake Erie for 1995–2011. Each piece of evidence comes from a unique dataset as reported for a specific year (ESM Tables S2 and S3). Methods for categorization of evidence for bloom absence or presence (A), for a bloom being localized or widespread (B), and for bloom onset, peak, and decline (C) are described in the ESM Appendix S1.

In 2002, above-threshold in situ chl a (DeBruyn et al., 2004) and toxigenic Microcystis DNA presence (Ouellette et al., 2006) seemingly contrast with relatively low Microcystis biovolume (Bridgeman et al., 2013) and remotely-sensed cyanobacteria (Stumpf et al., 2012) values (ESM Table S2). However, the chl a measurements are only slightly above the harm threshold, potentially due to other phytoplankton biomass, and the presence of toxigenic *Microcystis* DNA may occur even in "non-bloom" situations (Rinta-Kanto et al., 2009). In contrast, the biovolume and remote-sensing measurements point to 2002 as the least intense of the 2002-2011 period (i.e., closest to "non-bloom" conditions). This simple comparison between studies points out incongruences in the threshold for harm for each of these metrics. A strict interpretation using a conservative threshold for chl a might lead one researcher to categorize 2002 as a "bloom" year, while a comparison with other years shows 2002 to be closer to a "non-bloom" year. More broadly, the evidence from 2002 speaks to the limitations of binary presence/absence indicators relative to level or intensity indicators. Although binary designations provide convenient categories for further analysis, the threshold for harm clearly has a significant impact for years when the measurements are close to these thresholds.

A different insight arises from the evidence for 2004, with remote sensing evidence (from MODIS (Becker et al., 2009) and MERIS (Stumpf et al., 2012)) and most in situ evidence (from cell abundance (Dyble et al., 2008), chl a concentration (Millie et al., 2009), Microcystis DNA presence (Dyble et al., 2008; Rinta-Kanto et al., 2005), Microcystis percentage (Dyble et al., 2008; Millie et al., 2009; Rinta-Kanto and Wilhelm, 2006; Rinta-Kanto et al., 2009) and microcystin concentration (Boyer, 2008; Dyble et al., 2008; Millie et al., 2009; Rinta-Kanto et al., 2009)) supporting bloom presence and only a few pieces of evidence supporting bloom absence (ESM Table S2). The evidence for bloom absence, however, is noteworthy: two synoptic sampling cruises report no surface scum on the lake (Dyble et al., 2008; Millie et al., 2009), and, in particular, one study takes this lack of surface scum to be the key determinant in judging bloom absence for 2004, referring to 2004 as "a non-bloom year [despite] both Microcystis and microcystin widespread" (Dyble et al., 2008). Though a lack of surface scum is not definitive evidence of HAB absence, e.g., observations by Millie et al. (2009) come from only a few days in August, the statements by Dyble et al. (2008) demonstrate a subjective weighting given to different metrics in judging bloom occurrence. It is also notable that this weighting seems to be independent from the metric's linkage to harm (Fig. 1), which is important because metrics with indirect linkages to harm, such as surface scum presence, may not be reliable indicators of harmful impacts. Inasmuch as "bloom"/"nonbloom" designations are becoming part of the lexicon that drives further analysis in studying HABs, the evidence for 2004 suggests that such designations may be unreliable indicators of certain harmful impacts.

Overall, we find that a metric's threshold for harm and the subjective weighting given to each metric can have significant impacts on the determination of bloom occurrence in Lake Erie. This result, combined with the previous section's result that the linkages to harm are not immediately comparable across different metrics, suggests that there may not be as much basis for comparing the conclusions for bloom occurrence between studies as has been assumed in some of the literature (e.g., Becker et al., 2009 or Stumpf et al., 2012). Insofar as this

practice persists, the conclusions drawn from such comparisons may be overstated.

Size: How big was the HAB?

Assessing the size of blooms, and their maximum extent/intensity over the course of a season, is even more challenging than identifying bloom occurrence because in situ sampling (associated with abundance, toxicity, and qualitative metrics) can only be used to collect data at individual locations. For Lake Erie, the location where the measurements are taken is important because *Microcystis* blooms typically appear first and reach highest abundance in the transition zone between Maumee Bay and the deeper center of the western basin (Chaffin et al., 2011). Inferences on the size of blooms, therefore, depend not only on how data are interpolated but on the sampling locations. In this respect, there is great diversity in where in situ measurements are taken (Fig. 3). If such diversity leads to different conclusions about the expanse of big HABs, then understanding what factors contribute to greater HAB size could depend critically on not only the type of metric used but the sampling locations selected.

We synthesize the evidence on bloom extent from geospatial observations available in the literature (Fig. 2B; individual evidence from each study in ESM Table S2). The inferred spatial extent from each unique dataset per year is weighted as a single piece of evidence. For studies reporting in situ measurements at individual locations, the areal extent of the bloom is inferred by identifying which samples provide evidence for bloom presence; in other words, inferring the bloom extent based on "bloom" samples as determined in the previous section, similarly to Dyble et al. (2008). Though this approach provides only an approximate measure of extent as not all studies are designed for such inference, the results nonetheless provide a glimpse into how much is known about algal bloom extent in Lake Erie. A threshold of 1000 km² is selected as the threshold for a bloom being "widespread:" this is roughly 25% of the lake's western basin and the reported size of the bloom in 1995 which is

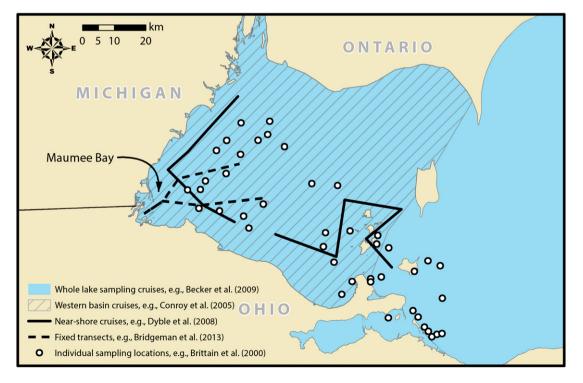


Fig. 3. Examples of the spatial distribution of in situ sampling. Examples of spatial coverage include whole-lake sampling cruises (e.g. Becker et al., 2009, light blue shading), cruises covering the western basin only (e.g. Conroy et al., 2005, hatched area), near-shore sampling cruises (e.g. Dyble et al., 2008, solid line), sampling limited to specific transects (e.g. Bridgeman et al., 2013, dashed line), and sampling at specific point locations (e.g. Brittain et al., 2000, white circles).

typically identified as the first bloom during the examined period (Budd et al., 2002). Note that in this framework a year can be designated as a "bloom" year (metric above threshold for occurrence, Fig. 2A), but the bloom might not be "widespread" (extent below threshold for large size, Fig. 2B). More detailed methodology is presented in the ESM Appendix S1.

The evidence for bloom extent is less clear than for bloom occurrence (Fig. 2B). For example, for two unanimous or near-unanimous bloom presence years identified previously (1995 and 2003, Fig. 2A), only a minority of studies provides evidence for whether or not the bloom was widespread (Fig. 2B). Even for record-setting blooms such as the one that occurred in 2011 (Michalak et al., 2013), estimates of the size or intensity of the bloom are variable. For example, Microcystis biovolume data suggests that the 2011 bloom was 2.4 times greater in intensity than the next largest bloom in 2008 (Bridgeman et al., 2013) whereas remotely-sensed cyanobacteria data suggests that it was 3.3 times more intense (Stumpf et al., 2012). Examining the evidence by method rather than by year (ESM Table S2) reveals the metrics that have provided clearer evidence about bloom extent, due primarily to differences in the spatial coverage of sampling conducted as part of studies using specific metrics. Studies based on chl a and microcystin concentrations, DNA-based metrics, and remotely-sensed metrics have mostly provided unambiguous evidence for bloom extent (either for widespread or localized blooms), while those based on sparser observations of mass and volume abundance, species-specific percentage, and surface scum presence have provided more ambiguous evidence.

This difference in the clarity of evidence can be explained by the locations where samples are taken and how the results are reported by each study. For example, three main studies out of the six total reporting abundance metrics either take samples too close to Maumee Bay to judge extent over the whole western basin (Bridgeman et al., 2013) or do not report geospatial information at all (Brittain et al., 2000; Conroy et al., 2005). This is in contrast to all four *chl a-*reporting studies, which cover enough of the Western basin to assess bloom extent and report the locations and values of individual samples (Davis et al., 2012; DeBruyn et al., 2004; Millie et al., 2009; Rinta-Kanto et al., 2005). This reflects the difficulty in comparing inferences from in situ sampled metrics across different studies that may use different sampling regimes and/or address different research questions (in addition to the different thresholds for harm identified previously).

Studies reporting remotely-sensed metrics seem to overcome sampling limitations by providing synoptic observations over the entire western basin, resulting in explicit estimates of bloom extent (e.g., Stumpf et al., 2012). Insofar as such metrics have sufficient frequency in time to capture the bloom, they appear promising. However, as has been indicated previously, remotely-sensed metrics have a less direct linkage to harm, and one that is often implicit rather than explicit. This means that, while they may provide better evidence for bloom extent, such metrics are more difficult to tie directly to the harmful impacts associated with HABs.

Overall, the published evidence on HAB extent in Lake Erie for 1995–2011 yields only a few clear assessments on how big blooms were during individual years (Fig. 2B). This ambiguity stems from some studies not reporting geospatial information and also from the difficulty in comparing evidence from different metrics, ultimately leading to less consensus than for "bloom"/"non-bloom" designations (Fig. 2A). This may explain why there have been few explicit comparisons of bloom size across years for Lake Erie. Although the need to better understand what causes widespread blooms has never been greater (especially in the wake of the record-setting HAB of 2011), the results here suggest that significant challenges remain in the search for reliable estimates of bloom size.

Timing: When did the HAB occur?

In addition to knowing whether a bloom occurred and how big it was, knowing when a bloom occurred is important both for pinpointing

causal factors for HABs and for developing proactive management policies. Consistent with the approach from the previous sections, we examine here the evidence for Lake Erie on bloom timing, specifically the dates at which blooms first occurred, peaked (i.e., reached maximum intensity), and declined.

We synthesize the evidence for bloom timing from different methods (Fig. 2C; evidence from individual studies in ESM Table S3). The bloom onset date is assumed to be when the metric first increases above the threshold for bloom presence, when the metric rises above subjectively-determined baseline levels (if no threshold exists for the metric), or when the original study authors explicitly report a date for bloom onset (more detailed methods in the ESM Appendix S1). Bloom peak and bloom decline are similarly defined as the time when the metric reaches a maximum and when it declines below the threshold (or returns to baseline), respectively.

In contrast to bloom occurrence and extent, there is much less evidence on bloom timing in the literature, with none at all for 1998–2001 (Fig. 2C). In general, this is due to in situ metrics providing limited information on timing other than presence/absence during the period when samples are taken. The exception is the study by Bridgeman et al. (2013), which reports results from samples taken every two weeks from late spring to early fall for 2002–2011. Remote sensing techniques also provide more evidence on timing, but the amount of information depends on the study. This is due to different research questions being explored by different researchers: the studies using SeaWiFS and MODIS, for instance, have focused on answering questions related to bloom occurrence rather than bloom timing (Becker et al., 2009; Dash, 2005).

The main evidence for bloom timing that does exist, from Stumpf et al. (2012) and Bridgeman et al. (2013) (the only multi-year studies presenting original data), seems to disagree, providing significantly different dates for bloom peak and decline (one-tailed *t*-test *p*-values <0.05, df = 18) (Fig. 4). The on-average earlier dates reported by Bridgeman et al. (2013), however, can at least partly be explained by the sampling locations used in that study, which are close to Maumee Bay (Fig. 3). Because the Microcystis blooms of this period typically start in Maumee Bay and drift east (Chaffin et al., 2011), the fact that synoptic evidence over the entire lake from Stumpf et al. (2012) would show a later peak and decline than Bridgeman et al. (2013) is not surprising. This seeming discrepancy nonetheless reveals a limited evidence base with which to further explore issues surrounding bloom timing. Without additional discussion on how best to define and measure the timing of blooms (and additional datasets with which to compare and contrast), exploring bloom timing will remain

More broadly, the general paucity of information on bloom timing can be attributed to the challenges associated with collecting data over a long period of time. For in situ metrics, there are a limited number of samples that can feasibly be collected in a given study; and, as it is the stated goal of many of these studies to map the spatial distribution of blooms in the lake, most studies opt for higher spatial, rather than temporal, coverage. The Bridgeman et al. (2013) study with high sampling frequency and limited spatial coverage takes the opposite approach, but still exemplifies this tradeoff in sampling strategy. Gathering evidence on bloom timing depends then both on limitations inherent to the method (i.e., feasibility of gathering data) and also on decisions made by the researchers (i.e., focusing limited data collection on answering certain questions).

The dearth of data on bloom timing for Lake Erie (Fig. 2C) reveals a lack of research on the temporal dynamics of HABs, something others have pointed out (Shen et al., 2012). Given the importance of temporal factors such as residence time in promoting HAB growth in Lake Erie (Michalak et al., 2013), this gap in the literature should be addressed. More long-term studies are needed to gain a better understanding of when blooms occur and the factors that influence bloom timing.

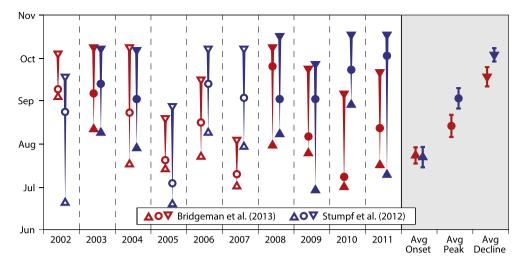


Fig. 4. Date of bloom onset, peak (circle) and decline based on data from Bridgeman et al. (2013) (red) and Stumpf et al. (2012) (blue). Because significant blooms did not appear in all years (Fig. 2A), "bloom" in this instance refers to increased cyanobacterial index/biovolume measurements above baseline (thresholds of 0.43 and 20 mL/m³, respectively from ESM Appendix S1). Filled and open symbols are years of bloom presence and bloom absence, respectively, as per the criteria described in the ESM Appendix S1. 2002–2011 average dates with standard-error bars (gray panel) show that average peak and decline are significantly different (one-tailed paired t-test p = 0.0488 and p = 0.0381, respectively, df = 18 for both).

Implications for future monitoring and research

Answers to basic questions about HAB occurrence, extent, and timing are found to strongly depend on the types of measurements used to support the analysis. This dependence occurs due to variations in sampling frequency, temporal coverage, and thresholds for harm, as previously noted by others (Steffen et al., 2014). This finding should at face value be surprising given that almost all monitoring methods are evaluated using cell abundances as a benchmark when first proposed and published, and the results of such evaluations often yield convincingly high correlations.

This observation points to the need for a more reliable approach for evaluating the consistency among monitoring approaches. For example, if methods are indeed intended to be used to determine HAB occurrence, extent, or timing, then comparing the conclusions about these features against those from other monitoring approaches would be a more natural basis for evaluation than sample-by-sample correlations. This approach would naturally include a discussion about comparable thresholds for harm, which have been notably absent thus far in the literature, although thresholds based on multiple metrics have been proposed by regulatory groups. Unfortunately, there are considerable challenges to implementing such an approach. For example, methods would need to be validated over several years, and data collection would need to capture bloom events accurately in the face of considerable uncertainty over when they occur in a given year. Although recent developments in autonomous HAB monitoring may help to address these challenges, such advances are still being tested and refined (Seltenrich, 2014).

A more reasonable approach may be to monitor the conditions under which different metrics are more, or less, consistent. For instance, McQuaid et al. (2011) report that the relationship between phycocyanin and cyanobacterial biovolume is much weaker when cyanobacteria are not dominant. Wynne et al. (2010) similarly report that remotely-sensed cyanobacteria measurements depend heavily on in situ meteorological conditions. In exploring the conditions under which metrics can effectively measure the outcome of interest, these studies contribute to greater understanding of how best to track HABs. An explicit evaluation of the comparability between metrics is, therefore, a natural initial step towards reconciling conclusions across measurement types, and would allow for deeper understanding of how different methods interrelate beyond what has been expressed in the literature (Fig. 1).

More broadly, the analysis presented here points to the poor comparability of binary designations such as "bloom"/"non-bloom" across different metrics, especially those that do not have clearly-defined harm thresholds. At a minimum, there is a need to be explicit about what thresholds for harm are being used, and to make raw data accessible so that others can apply alternate thresholds for harm if necessary. When comparing conclusions across different studies is necessary, the factors that may limit comparability must be explicitly recognized (e.g., metric value relative to the threshold for harm, spatio-temporal coverage of samples, and/or how closely the study's metric is linked to harm). More research on addressing the factors that limit the comparability between metrics would lead to better understanding of conditions under which binary designations are more or less comparable, and ultimately to better approaches for addressing the challenges of tracking HABs.

The conclusions presented here suggest an even greater challenge for researchers developing mechanistic or statistical models to understand the causal factors that influence HABs. As such models are developed and validated on the basis of correspondence with in situ or remotely-sensed data on bloom occurrence, extent, and timing, the lack of comparability among different types of measurements raises questions about the basis of information used in model development. If conclusions on bloom occurrence, extent, and timing vary across metrics, it should be expected that models calibrated to different metrics will also vary in terms of their conclusions about controlling processes, as well as the functional forms and parameterizations of these processes within the models. Data-driven model development efforts would therefore benefit substantially from further research on the robustness of such models and their conclusions to different bloom metrics.

This review has focused on the literature for Lake Erie, where the state of science is as good as, or better than, in most freshwater ecosystems. We note, however, the emergence of a similar diversity of monitoring methods for other systems, such as for Lake Taihu (Chen et al., 2003; Shen et al., 2003; Song et al., 2007) and Lake Victoria (Lung'Ayia et al., 2000; Ochumba and Kibaara, 1989; Sitoki et al., 2012), with the same sample-by-sample correlations being used for validation of methods (e.g., Sitoki et al., 2012; Song et al., 2007). Furthermore, although there has been less emphasis on binary designations of "bloom"/"non-bloom" in other systems, this may change as watershed managers implement bloom mitigation strategies in some regions, and as global climate change leads to bloom re-emergence in

others. Therefore, the conclusions drawn here about the impact of variations in harm thresholds, sampling regime, and linkage to harm apply to other freshwater ecosystems as well.

Overall, the case of Lake Erie provides insights into how basic questions about HABs might be answered based on the existing literature. We find that there are significant challenges in tracking harmful algal blooms, stemming from the difficulty in comparing results across a diverse set of metrics. Although the analysis conducted here applies most directly to freshwater cyanobacterial HABs, the identified challenges largely also apply to other systems and other types of HABs. Addressing these challenges by better understanding the interplay between different metrics is necessary for tackling more complex questions about the causes and future of HABs, thereby providing a path towards halting, and hopefully reversing, the trend towards more frequent and intense HABs globally.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jglr.2015.01.001.

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