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Toxic benthic freshwater cyanobacterial proliferations: Challenges and solutions for enhancing knowledge and improving monitoring and mitigation

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Abstract

1. This review summarises knowledge on the ecology, toxin production, and impacts of toxic freshwater benthic cyanobacterial proliferations. It documents monitoring, management, and sampling strategies, and explores mitigation options.

2. Toxic proliferations of freshwater benthic cyanobacteria (taxa that grow attached to substrates) occur in streams, rivers, lakes, and thermal and meltwater ponds, and have been reported in 19

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countries. Anatoxin- and microcystin-containing mats are most commonly reported (eight and 10 countries, respectively).

3. Studies exploring factors that promote toxic benthic cyanobacterial proliferations are limited to a few species and habitats. There is a hierarchy of importance in environmental and biological factors that regulate proliferations with variables such as flow (rivers), fine sediment deposition, nutrients, associated microbes, and grazing identified as key drivers. Regulating factors differ among colonisation, expansion, and dispersal phases.

4. New -omics-based approaches are providing novel insights into the physiological attributes of benthic cyanobacteria and the role of associated microorganisms in facilitating their proliferation.

5. Proliferations are commonly comprised of both toxic and non-toxic strains, and the relative proportion of these is the key factor contributing to the overall toxin content of each mat.

6. While these events are becoming more commonly reported globally, we currently lack standardised approaches to detect, monitor, and manage this emerging health issue. To solve these critical gaps, global collaborations are needed to facilitate the rapid transfer of knowledge and promote the development of standardised techniques that can be applied to diverse habitats and species, and ultimately lead to improved management.

Keywords

cyanotoxins; ecology; lakes; monitoring; risk assessment; rivers; toxin production

1. INTRODUCTION

Toxic benthic freshwater cyanobacterial proliferations were first documented and associated with animal poisonings in the 1990s (Edwards, Beattie, Scrimgeour, & Codd, 1992; Gunn et al., 1992). Over the last 2 decades, there has been an increase in the number of toxin-producing benthic cyanobacterial species identified and associated animal poisonings (Bouma-Gregson, Kudela, & Power, 2018; Cantoral Uriza, Asencio, & Aboal, 2017; Gugger et al., 2005; McAllister, Wood, & Hawes, 2016; Quiblier et al., 2013). This is reflected to some degree by the increase in publications on benthic cyanobacteria in the last 5 years, although these are not increasing at the same rate as for planktonic blooms (Figure 1). Most of the work published to-date has focused on characterising the toxin-producing cyanobacteria and their toxins (e.g. Cadel-Six et al., 2007; Wood, Heath, Holland, et al., 2010). Currently, there is a limited understanding of the: (1) environmental conditions promoting toxic benthic cyanobacteria proliferations; (2) life cycle of a toxic benthic proliferation (from the initiation of the biofilm to its detachment and fate); and (3) influences of environmental variables on genotype composition and the spatial and temporal dynamics of toxin production. This is partly due to a lack of standardised approaches to monitor, manage and mitigate benthic cyanobacterial proliferations.

There are many parallels between toxic benthic cyanobacteria proliferations and their planktonic counterparts. For example, both are often dominated by a restricted number of species and can include both toxic and non-toxic strains of the same species. Additionally,

there is spatial and temporal variability in toxin concentrations, and geographically separated species can produce different toxins. Finally, interactions with associated heterotrophic bacteria play an important role in regulating growth and bloom/proliferation formation. However, not all techniques from research on planktonic proliferations can be transferred and novel approaches are required for benthic cyanobacterial research, largely due to their biofilm growth form.

Numerous papers have been published since the first comprehensive review on toxic freshwater benthic cyanobacteria in 2013 (Quiblier et al., 2013). This review summarises the progress that has been made, highlights the knowledge gaps that remain and identifies critical areas for future research regarding toxic benthic freshwater cyanobacteria. It is divided into four sections; autecology; ecosystem and human health impacts; monitoring, sampling, and sample analysis; and mitigation strategies. In the autecology section, knowledge on the identity and distribution of toxin-producing benthic freshwater cyanobacteria species is reviewed. We summarise understanding of the drivers of proliferations and the factors that affect toxin production and concentrations. This section also covers studies on toxic benthic cyanobacteria which have incorporated -omics techniques. The second section explores the effects of toxic benthic cyanobacteria on ecosystem health and animal health. In the monitoring, sampling, and sample analysis section, monitoring approaches that have been implemented and new technologies are summarised, and sample collection and analysis methods are also evaluated. In the final section, we review approaches to managing benthic cyanobacterial proliferations and call for global collaborations to efficiently respond to this emerging environmental problem.

2. AUTECOLOGY OF TOXIC BENTHIC CYANOBACTERIA

2.1 General characteristics of toxic benthic cyanobacterial proliferations

Toxic benthic cyanobacteria occur in lakes, reservoirs, streams, rivers, meltwater, and geothermal ponds (Table 1, Figure 2). They grow on sand, cobbles, bedrock, wood, and epiphytically on aquatic plants (Table 1). They can spread laterally across the substrate (Heath, Wood, Brasell, Young, & Ryan, 2015) or accrue vertically with mats >70 cm thick reported (Dasey et al., 2005). Genera that commonly contain toxin-producing benthic species include; *Anabaena*, *Nostoc*, *Oscillatoria*, *Phormidium* (now also known as *Kamptonema/Microcoleus*), *Microcoleus*, and *Microseira* (previously *Lyngbya*). A large number of species have now been confirmed as toxin producers or have been associated with toxin-containing mats (Table 1). Benthic proliferations usually include non-toxic taxa, but toxin-producing species can be dominant or co-dominant (Heath, Wood, & Ryan, 2010).

Toxic benthic cyanobacteria have now been reported in 19 countries, with benthic anatoxin production reported in eight countries, and benthic microcystin (MCY) or nodularins (NODs) production documented in 10 countries. The production of cylindrospermopsins (CYNs) by a benthic species has been reported in Australia (Figure 2). Some species produce different toxins based on their geographic locations; e.g. *Microseira wollei* (Farlow ex Gomont) G.B.McGregor & Sendall ex Kenins [basionym *Lyngbya wollei* (Farlow ex Gomont) Speziale & Dyck] produces CYNs in Australia (Seifert, McGregor, Eaglesham, Wickramasinghe, & Shaw, 2007), but in Canada (Lajeunesse et al., 2012) and the U.S.A.

it produces saxitoxins (SXTs; Mihali, Carmichael, & Neilan, 2011; Smith, Martin, Wei, Wilhelm, & Boyer, 2019).

2.2 Phenology of benthic cyanobacteria proliferations

The general accrual cycle for benthic cyanobacteria typically involves: (1) initiation of a mat through colonisation by filaments or hormogonia that settle on a substrate, or regrowth of relic populations; (2) subsequent growth through increase in thickness, or lateral expansion; and (3) detachment of mats (Echenique-Subiabre, Tenon, Humbert, & Quiblier, 2018; McAllister et al., 2016). After colonisation, the balance of growth- and loss-promoting factors determines the length of the accrual cycle, and the size and persistence of the proliferation. Flow, nutrient, and temperature dynamics interact to determine the phenology of benthic cyanobacteria accrual (McAllister, Wood, Atalah, & Hawes, 2018; Wood, Atalah, et al., 2017), but our understanding of these physiochemical drivers is limited to a few species and habitats. Given the high biodiversity of benthic cyanobacteria and the diverse habitats they occur in, it is likely that they use many different strategies to optimise growth and survival. One of the most researched toxic benthic cyanobacteria is *Microcoleus autumnalis* (Gomont) Strunecky, Komárek & J.R.Johansen (basionym *Phormidium autumnale*). This genus has become problematic worldwide (Bouma-Gregson et al., 2018; Echenique-Subiabre, Tenon, et al., 2018; McAllister et al., 2016). In the following analysis, we use our knowledge of *M. autumnalis* and the genus *Phormidium* to describe a generalised accrual cycle for benthic cyanobacteria proliferations. The progression of proliferation and the methods developed for monitoring *Phormidium* can inform research on other genera.

The initiation of the *M. autumnalis* accrual cycle can involve colonists from the overlying water column or residual populations remaining on the substrata after the termination of the previous cycle (McAllister et al., 2016). There is a dearth of research on the colonisation stage in *M. autumnalis*, but physical factors such as flow dynamics, sheer stress, and substrate size and mobility are likely to determine the suitability of a given habitat for colonisation (McAllister, Wood, Atalah, et al., 2018; Stevenson, 1983). The biomass of upstream populations affects propagule density (Bouma-Gregson, Power, & Bormans, 2017), and once a habitat has been colonised previously it appears to have a greater propensity for subsequent proliferations (McAllister, Wood, Atalah, et al., 2018). Once colonising cells adhere to a surface, competition with other benthic photoautotrophs and herbivory may deter establishment and reduce growth rate, but we found no information on biological determinants of colonisation success.

Once a habitat has been colonised, physicochemical conditions strongly determine the growth and expansion rate of *M. autumnalis* and *Phormidium* proliferations. Current velocities between 0.3 and 0.8 m/s have been shown to favour *M. autumnalis* and *Phormidium* growth in streams (Echenique-Subiabre, Tenon, et al., 2018; Hart, Biggs, Nikora, & Flinders, 2013; Heath et al., 2015; McAllister, Wood, Mackenzie, & Hawes, 2019). In experimental stream mesocosms, McAllister, Wood, Greenwood, Broghammer, and Hawes (2018) found that those with lower velocities (0.1 compared to 0.2 m/s) had less biomass accrual. It is likely that velocity affects both resource availability and grazing

intensity. As velocity increases, the diffusional boundary layer around the mat decreases, allowing greater movement of solutes in and out of the mat matrix. Velocity also affects the assemblage of grazers in a given habitat and may influence their effectiveness (Hart et al., 2013; McAllister et al., 2019).

Microcoleus autumnalis and other species belonging to the genus *Phormidium* proliferate under a wide range of nutrient conditions, from eutrophic lakes to oligotrophic rivers and lakes (i.e. Loza, Berrendero, Perona, & Mateo, 2013; Loza, Perona, Carmona, & Mateo, 2013; Loza, Perona, & Mateo, 2013; Monteagudo & Moreno, 2016; Takano, Igarashi, Mikami, & Hino, 2003; Voorhies et al., 2012). Echenique-Subiabre, Tenon, et al. (2018) found that proliferations of *Phormidium* occurred with nitrate concentrations of 1.46 mg/L, whereas McAllister, Wood, Atalah, et al. (2018) and Wood, Atalah, et al. (2017) found that proliferations occurred when dissolved inorganic nitrogen concentrations were as low as 0.02 mg/L. Concentrations of dissolved reactive phosphorus in the water column below 0.05 mg/L have been shown to favour *M. autumnalis* proliferation over other periphyton in New Zealand streams (McAllister, Wood, Atalah, et al., 2018). However, phosphorus concentrations within *M. autumnalis* mats can be over 300 times higher and this may explain how such high biomass can occur within relatively low nutrient (<0.01 mg/L) overlying waters (Wood, Depree, Brown, McAllister, & Hawes, 2015). While photosynthetic depletion of bicarbonate elevates the pH (>9) in the mat during the day, respiration depletes oxygen (<4 mg/L) at night, creating conditions conducive to the release of iron-bound dissolved reactive phosphorus in sediment. Recent molecular analysis has shown that *Microcoleus* also has the ability to undertake alkaline phosphatase activity, and therefore it is likely that organic phosphate also provides an important source of this nutrient.

There is general agreement *M. autumnalis* and *Phormidium* proliferations are positively correlated with temperature (Echenique-Subiabre, Tenon, et al., 2018; Heath, Wood, & Ryan, 2011; Schneider, 2015; Wood, Atalah, et al., 2017). However, the occurrence of *Microcoleus/Phormidium* in polar regions shows that low temperatures do not preclude biomass accrual, rather they slow the speed at which proliferations develop (i.e. Taton et al., 2006). Light also impacts *Phormidium* growth with high light in shallow areas allowing biofilms to increase in thickness while the lower light availability at depth promoted lateral expansion (Echenique-Subiabre, Tenon, et al., 2018).

A relatively unexplored factor is the effect of top-down controls on *M. autumnalis* growth. Herbivory is known to be important in regulating periphyton community composition and biomass (Anderson, Welch, Jacoby, Schimek, & Horner, 1999; Karouna & Fuller, 1992; Vadeboncoeur & Power, 2017). The snail, *Potamopyrgus antipodum*, was more abundant on patches of *Phormidium* than on patches of green algae (Hart et al., 2013), and increased abundances of grazing macroinvertebrates have been associated with reduced patch size in *Microcoleus* (McAllister et al., 2019); however, actual consumption of the filaments by herbivores has not yet been demonstrated. The long filamentous morphology of many benthic cyanobacterial species may make them less palatable than diatoms or green algae (Scott & Marcarelli, 2012). Preferential consumption of diatoms or green algae may open up new space for colonisation. Conversely, Hart (1985) describes how a caddisfly larva

(*Leucotrichia pictipes*) removed, but did not ingest, filaments of *Microcoleus*, which in turn facilitated growth of preferred food items.

After a period of growth and expansion, cyanobacterial proliferations often dissipate abruptly. Early research attributed the dissipation of proliferations almost exclusively to increases in river flow, with the intensity of flow required to remove mats being site-specific (Wood, Atalah, et al., 2017). Many observational studies and manipulative experiments have shown that autogenic detachment also terminates accrual cycles (Bouma-Gregson et al., 2017; McAllister, Wood, Atalah, et al., 2018; McAllister et al., 2019; Sabater et al., 2003). This phenomenon may be related to the entrapment of oxygen bubbles within the mat matrix, increasing buoyancy and causing the biomass to detach from the substrate and float to the surface where it can accumulate along the banks of the river or stream (Bouma-Gregson et al., 2017; Mendoza-Lera, Federlein, Knie, & Mutz, 2016). Gas bubble formation within the mat matrix is more likely under low flow regimes, since diffusion of oxygen out of the mat will be slowed by the existence of a thick boundary layer (McAllister, Wood, Greenwood, et al., 2018).

Further research identifying drivers of toxic benthic proliferations in a greater number of toxic species, and from diverse habitats, is required to identify commonalities and differences among taxa. There is a need for more manipulative experimental studies to explore hypotheses that have been developed based on correlative field studies. The use of -omics techniques (discussed below) is now providing new insights into the physiology of cyanobacteria and other microbes within the mats and there is a need for more studies that incorporate these methods in parallel with traditional approaches.

2.3 Drivers of toxin production and variability

Elucidating the drivers of toxin production and variability will improve awareness among water managers on the public health risks of benthic cyanobacterial proliferations. Such research requires standardised sampling, processing, and analytical techniques for quantifying cyanotoxin concentrations; however, methods developed for planktonic proliferations are not easily applied to benthic mats. Water column concentrations of cyanotoxins are generally expressed per volume of water or per cell but because benthic proliferations spread laterally over time, they are characterised by enormous spatial variability in area-specific cyanobacterial biomass (Figure 3). This spatial heterogeneity makes it difficult to interpret biomass-specific toxin concentration of point samples. Method development and standardisation must be a priority. To date, our understanding of drivers of toxin production is based on sampling of benthic mats in situ (usually expressed as toxin/dry mass) and culture-based studies. The effect of most environmental factors, such as light and temperature on toxin production has not been studied in benthic species.

A new approach that has been developed for culture-based studies on benthic species is to inoculate many individual culture vessels with a known wet weight of starting material and at each time point an entire culture vessel is sacrificed for analysis. The sample is homogenised and subsampled for cell counts and extra- and intracellular cyanotoxin analysis (Harland, Wood, Moltchanova, Williamson, & Gaw, 2013; Heath, Wood, Barbieri, Young, & Ryan, 2014; Heath, Wood, Young, & Ryan, 2016). These culture studies have

been instrumental in demonstrating that toxin production varies with growth stage and is influenced by nutrient availability. For example, anatoxin quotas in *M. autumnalis* were highest during the early exponential phase suggesting that anatoxins may provide a physiological benefit during initial substrate colonisation (Heath et al., 2014; Heath et al., 2016). In batch culture experiments, the slow-growing benthic species *Scytonema* cf. *crispum* produced the highest saxitoxin quotas during the lag phase, followed by the exponential phase (Harland, Wood, Broady, Williamson, & Gaw, 2015). Cellular quotas for anatoxin in *M. autumnalis* were lowest under high-nitrate and high-phosphate and highest in reduced phosphate treatments (Heath et al., 2016), suggesting that anatoxins are produced as a stress response to nitrogen- and phosphorus-limiting conditions. Heath et al. (2014) interrogated the data from the same experiment and explored how anatoxin variants change under these different nutrient regimes. Dihydroanatoxin-a (dhATX) quotas decreased significantly when nitrogen and phosphorus concentrations were elevated, while homoanatoxin-a (HTX) quotas increased when the phosphorus concentrations were reduced. In contrast to N and P, iron concentrations between 40 and 800 μg/L and copper concentrations between 2.5 and 250 μg/L had no effect on anatoxin production by *M. autumnalis* (Harland et al., 2013).

In addition to the amount of toxin produced by a cell, toxin concentrations within benthic mats depend upon the relative abundance of toxic and non-toxic genotypes in the assemblage, which is similar to planktonic cyanobacterial proliferations (O'Neil, Davis, Burford, & Gobler, 2012). Benthic cyanobacterial-dominated mats are commonly a mixture of toxic and non-toxic strains (Heath et al., 2010, 2011). Using a droplet digital polymerase chain reaction (PCR) species-specific *anaC* assay in concert with liquid chromatography–tandem mass spectrometry (LC-MS/MS), several studies have shown that the variability in anatoxin concentrations among *Microcoleus* -dominated mats is primarily due to the relative abundance of toxic genotypes (Wood & Puddick, 2017). Factors that cause toxic or non-toxic strains to become dominant in a mat are unknown but culture-based studies have shown that maximum growth rates were higher for a *Microcoleus* strain lacking the ability to produce anatoxin compared to an anatoxin-producing strain under a range of nitrogen and phosphorus treatments suggesting there may be an energetic cost to toxin production (Heath et al., 2016).

3. ECOSYSTEM AND HUMAN HEALTH IMPACTS

3.1 Effects and accumulation of benthic cyanobacterial toxins in aquatic organisms

To date, few studies have explored the effect of cyanotoxins on benthic organisms. Toporowska, Pawlik-Skowrońska, and Kalinowska (2014) investigated the impacts of crude planktonic cyanobacterial extracts (containing low concentrations of cyanotoxins) and purified MCY and anatoxin-a (ATX) on *Chironomus* spp. larvae, finding greater mortality on exposure to crude extracts than purified toxins. This suggests that compounds produced by cyanobacteria other than the known toxins are likely to have a negative effect on some aquatic organisms. Anatoxin-a, dhATX, and HTX/dihydro-HTX purified from environmental *Microcoleus* -dominated mats had no acute effects on *Deleatidium* spp. (mayfly) larvae (Kelly, Puddick, Ryan, Champeau, & Wood, 2019). In contrast,

Anderson et al. (2018) showed that acute exposure to crude *Phormidium* extracts containing ATX resulted in significant mortality in three macroinvertebrate taxa (*Chironomus dilutus*, *Ceriodaphnia dubia*, and *Hyalella azteca*), adding further evidence to support the presence of harmful compounds other than known toxins. Sublethal effects of benthic cyanobacteria and their cyanotoxins have not yet been investigated and this should be a priority for future research. For example, research is required on the effects on fecundity and the ability of aquatic organisms to complete their lifecycle (especially in the case of emergent macroinvertebrates).

Significant knowledge gaps remain regarding the potential for benthic cyanotoxin accumulation up trophic levels (both aquatic and terrestrial). In a laboratory study using the mayfly *Deleatidium* spp., larvae exposed to high concentrations of purified dhATX accumulated the toxin (Kelly, Puddick, et al., 2019). Mayflies are prey for a range of fish species, and the possibility of trophic transfer of anatoxins and pathways for toxin assimilation in environmental samples should be investigated. An additional concern is the risk of human exposure to cyanotoxins in food gathered from freshwaters. Kōura (freshwater crayfish; *Paranephrops planifrons*) are a culturally significant food source in New Zealand and nodularin from benthic mats have been shown to accumulate in the hepatopancreas and tail tissue (Wood, Phillips, de Winton, & Gibbs, 2012). Preliminary analysis of fish collected from French rivers during benthic cyanobacterial proliferations has revealed the presence of anatoxins in muscle, gut, and encephalon (Colas, Duval, & Marie, 2019).

3.2 Effects on livestock and animals

The most frequently reported animal deaths linked to benthic cyanobacteria exposure are dogs who consume biofilms dominated by anatoxin-producing *Microcoleus*, *Phormidium*, or *Oscillatoria* (Bouma-Gregson & Higgins, 2015; Edwards et al., 1992; Faassen, Harkema, Begeman, & Lurling, 2012; Fastner et al., 2018; Gugger et al., 2005; Puschner, Hoff, & Tor, 2008; Wood, Puddick, Fleming, & Heussner, 2017; Wood et al., 2007). In these instances, the dogs were probably attracted to the musty aroma of the cyanobacteria (due to compounds such as geosmin and 2-methylisoborneol) and therefore ingested a high dose of toxins. Whilst anatoxins are the more frequently reported causative toxin in benthic cyanobacteria animal poisoning cases, MCY produced by *Planktothrix* (Wood, Heath, Holland, et al., 2010) and other benthic consortiums (Mez et al., 1997) have also been implicated.

In addition to direct ingestion of mat material, a further exposure route is the release of toxins from benthic cyanobacteria into the surrounding water. Wood, Biessy, and Puddick (2018) recently investigated whether this occurred with *Microcoleus* proliferations in New Zealand rivers and found that anatoxins were consistently released from the mats, but not at levels that were likely to cause adverse effects to livestock and animals.

4. MONITORING, SAMPLING AND SAMPLE ANALYSIS

4.1 Traditional proxies for biomass

Benthic cyanobacterial biomass assessment is typically undertaken by visual estimates of percentage cover using an bathyscope (underwater benthic viewer) along set transect lines or quadrats (Wood, Hamilton, Paul, Safi, & Williamson, 2009). However, these assessments do not consider mat thickness, or make only a coarse assessment, i.e. thin biofilm, 5 mm thick. Despite this, there are indications that some species, such as *M. autumnalis* expand laterally rather than increasing in thickness, as there is a good correlation between percent cover and total biomass (as determined by chlorophyll-*a*) (Echenique-Subiabre, Tenon, et al., 2018; McAllister, 2018).

Chlorophyll-*a* (reported as mg m^{-2}; Snow, 2016) is generally used as a proxy for benthic algal biomass. As with all measures of chlorophyll during cyanobacterial blooms/proliferations, some caution is needed as chlorophyll content per cell varies with species and with incident light level, and because cyanobacterial mats often contain many other eukaryotic algae, it does not necessarily provide a measure of cyanobacterial biomass. Cyanobacterial-specific accessory pigments phycoerythrin and phycocyanin are a better proxy for cyanobacteria biomass within benthic mats (McAllister, 2018).

Small portable fluorometers such as the BenthoTorch (bbe Moldaenke GmbH, Germany, Echenique-Subiabre et al., 2016; Kahlert & McKie, 2014) can provide semi-quantitative data on total in situ chlorophyll-*a* concentration as well as distinguish between three taxonomic groups—cyanobacteria, diatoms, and green algae. It is placed underwater directly on benthic mats (Echenique-Subiabre et al., 2016; Kahlert & McKie, 2014). A strong correlation between BenthoTorch derived concentrations and *Microcoleus* biovolumes has been reported during the early stages of mat development (<2 mm), but the relationships weakened once the mats increased in thickness (Echenique-Subiabre et al., 2016). These authors attributed this to the BenthoTorch measuring only the upper biofilm layer and underestimating the biomass of phycoerythrin-containing cyanobacteria deeper in the mat.

4.2 Remote Sensing

In vivo, chlorophyll-*a* can also be used at lower resolutions for biomass assessments via remote sensing applications including satellite imagery and unmanned aerial vehicles with a variety of sensors including red-green-blue, multi-spectral and hyperspectral sensors in the visible and near infrared light range. Unmanned aerial vehicles are a potentially new platform for automated calculation of benthic algal coverage. There are challenges with the use of unmanned aerial vehicles for this purpose due to difficulties with optical discrimination of benthic cyanobacteria from in-organic material and the effects of reflection and distortion from the rippling surface of the water. In the visible spectrum, cyanobacteria exhibit relatively low reflectance and appear black or dark green. While a contrast with river substrate of higher reflectance is easily distinguished, the substrate is often highly variable in reflectance and shadows cast by rocks or other objects cannot be readily discriminated in visible-spectrum images from cyanobacteria (Figure 3; Hempel, Heath, Olds, Wood, & Ryan, 2014). Aerial red-green-blue imagery is sometimes sufficient to

identify cyanobacterial proliferations and, from these, it is possible to estimate percentage cover, although the thickness of the mat cannot be determined. Hyper-spectral imaging involves a relatively high-resolution spectrum (wavelengths of 2–10 nm) being collected for each pixel in the image. Hyper-spectral imaging allows for the estimation of the content of chlorophyll-*a* and other cyanobacterial pigments in water bodies (Hall, Bostater, & Virnstein, 2004; Hunter, Matthews, Kutser, & Tyler, 2017; Hunter, Tyler, Carvalho, Codd, & Maberly, 2010). It is also possible, with appropriate algorithms, to separate different cyanobacterial genera using this technology (Kudela et al., 2015). A new low-cost sensor based on three-band indices and able to detect phycocyanin- and phycoerythrin-rich cyanobacteria has been recently developed for the monitoring of planktonic and benthic cyanobacteria (Hmimina et al., 2019) but is not yet commercially available.

4.3 Omics techniques and applications in toxic benthic cyanobacterial research

Benthic mats are complex microbial assemblages comprising bacteria, algae, eukaryotic organisms, and inorganic material in addition to cyanobacteria, all of which can change across successional cycles (Brasell, Heath, Ryan, & Wood, 2015). The use of -omic tools (e.g. metabarcoding, genomics, transcriptomics, proteomics, metagenomics, metatranscriptomics, metaproteomics, and metabolomics) is expanding rapidly and is providing many valuable insights into the composition and function of these dynamic communities. Examples of the application of these methods to toxic benthic cyanobacterial research are limited. Metabarcoding (a method of DNA barcoding that enables the amplification of DNA and identification of a mixture of organisms from a sample) has been used to explore bacterial communities in *Microcoleus* -dominated mats from New Zealand and French streams (Echenique-Subiabre, Zancarini, et al., 2018). These studies showed that despite the differences in bacterial community composition between sites; at phyla, class, and order levels there was high similarity across spatial scales, with Bacteroidetes and Proteobacteria dominant. Bouma-Gregson et al. (2019) undertook the first metagenomic (the direct genetic analysis of genomes contained with an environmental sample) study of toxic cyanobacteria mats in the Eel River (California, U.S.A.). The authors showed that many of the heterotrophic bacteria within the mats had metabolic capacities, such as oxygenic and anoxygenic photosynthesis, carbon respiration, sulfur compound oxidation, and breakdown of organic nitrogen (e.g. urea), which may benefit *Microcoleus* through the internal cycling of nutrients.

In the first proteogenomics (the integration of proteomics with genomics and transcriptomics) study of toxic benthic cyanobacteria, *Microcoleus* -dominated mats were tracked through a 19-day proliferation (Tee et al., 2020). Although *Microcoleus* species dominated the mats, proteomics data showed that a mixture of phototrophs (other cyanobacteria and diatoms) competed for resources, and organic and inorganic molecules generated within the mat were actively recycled by a small group of Bacteroidetes. *Microcoleus* acquired nitrogen by nitrate and urea uptake from the water, and stored, or accessed, nitrogen and carbon from internal cyanophycin granules. Organic and inorganic phosphorus were scavenged by *Microcoleus* from the biofilm and the water within. *Microcoleus* also contained genes for inorganic phosphate solubilisation, which could be used in conjunction with pyrroloquinoline quinone cofactors produced by co-habiting

Proteobacteria. The ability of *Microcoleus* to use multiple sources of nutrients may explain how it thrives in relatively low nutrient waters. These techniques will be invaluable in future studies that aim to understand drivers of proliferation.

4.4 Sampling Strategies for Toxic Benthic Cyanobacteria

There is often significant spatial variability in toxin content in mats (Wood, Biessy, et al., 2018; Wood, Heath, Kuhajek, & Ryan, 2010). To reduce costs and obtain a representative assessment of toxins at a site scale for genetic or chemical analysis or for taxonomic identification, it may be advisable to take a representative sample from multiple places which can then be homogenised. For *Microcoleus*, Wood, Heath, Kuhajek, et al. (2010) recommended that 10 samples be taken to increase the likelihood of toxin been detected at a given site. Similar studies have not been undertaken for other toxin-producing benthic taxa.

When collecting water samples for the analysis of cyanotoxins, standard sampling practices (e.g. grab samples) provide only a snapshot (in space and time) and may miss areas or times of highest occurrence and therefore risk. To overcome these challenges, the use of solid-phase adsorption toxin tracking (SPATT) samplers has been applied (Miller et al., 2010; Roué, Darius, & Chinain, 2018; Wood, Holland, & MacKenzie, 2011). This method allows toxins dissolved in the water to bind to an absorbent material suspended in fine mesh. The sampler can be left in the water for hours to weeks—providing a time integrated measure, and after collection the toxins are extracted from the absorbent material for analysis. These sampling devices have been successfully used to understand the distribution of cyanotoxins in the Eel River network in northern California (U.S.A.) (Bouma-Gregson et al., 2018) and to assess the release of anatoxins in New Zealand rivers (Wood, Biessy, et al., 2018). The toxin concentrations obtained from SPATT should not be considered as quantitative as the SPATT is likely to become saturated (by toxins and other organic compounds), and toxins adsorbed to the resin may degrade over time.

4.5 Analytical measurement of cyanotoxins and toxic cyanobacteria in benthic proliferations

Whilst cyanotoxins from benthic cyanobacteria can be analysed using the same analytical methods used to assess toxins from planktonic cyanobacteria, the solid matrix of the benthic mats requires more thorough and standardised homogenisation prior to subsampling than a water sample containing planktonic material. Freeze-drying of samples prior to homogenisation can help to break down the macro-structure of the mats, which can be difficult with a wet sample. Conventional extraction methods such as freeze-thawing for hydrophilic toxins (e.g. anatoxins) and the use of organic solvents for more hydrophobic toxins (e.g. MCYs) are suitable, but the more complex nature of the benthic material can result in matrix effects and low recoveries. Benthic cyanobacteria samples from the Arctic region of Svalbard, that tested positive for MCY by enzyme-linked immunosorbent assay (ELISA), were also assessed using a LC-MS/MS precursor ion screening method (Kleinteich et al., 2018). Only 58% of the samples that tested positive by ELISA were determined to contain MCYs, a 42% false-positive rate. Whilst the complex sample matrix can cause false positives with ELISA tests, it can cause ionisation suppression effects with

MS-based quantitation methods resulting in lower than expected results. More thorough sample clean-up would probably improve the accuracy of both analytical methods.

Another strategy to overcome the effects of complex sample matrices and poor recoveries from sample clean-up procedures (with MS-based testing) is the use of an internal standard. This is a compound nearly identical to the compound being analysed but distinguishable by several mass units. This strategy was recently applied to the analysis of MCYs in another complex matrix—plasma and liver samples (Altaner et al., 2019)—and might be of benefit for the analysis of benthic cyanobacteria samples. The main drawback with this approach is the limited availability of internal standards.

With highly specific toxin detection techniques such as LC-MS/MS multiple-reaction monitoring (MRM) methods, there is a likelihood that other toxin congeners present in the sample may be missed (Puddick, Thomson-Laing, & Wood, 2019). New structural modifications of MCYs have been observed in benthic *Nostoc* species including the acetyl-desmethyl modification of the Adda amino acid (ADMAdda) (Beattie, Kaya, Sano, & Codd, 1998; Fewer et al., 2007; Kaasalainen et al., 2012; Puddick et al., 2015). As a fragment of the Adda moiety is commonly used as a target ion in LC-MS/MS MRM, the ADMAdda-containing MCYs are not detected. This was the case in benthic mat samples from the Dry Valleys of Antarctica, which contained ADMAdda moieties, dehydrobutyrine, homoarginine residues, and a rare position-1 glycine (Puddick et al., 2015; Wood et al., 2008). Many of these congeners were not detected using standard LC-MS/MS MRM methods for MCYs. In these instances, the use of less-specific detection techniques such as a MS/MS precursor ion screen, with detects ions with characteristics of MCs (Kleinteich et al., 2018) or ELISAs, may be useful for a preliminary screen although false positives will need to be checked. Geographic differences in the congener profiles of anatoxins produced by *Microcoleus* or *Phormidium* have also been observed between New Zealand, France, and U.S.A. (Echenique-Subiabre, Tenon, et al., 2018; Kelly, Bouma-Gregson, et al., 2019; McAllister et al., 2016); highlighting the continued need for exploratory work on toxins from benthic cyanobacteria.

As benthic cyanobacteria mats are generally a complex assemblage of multiple organisms and other components, normalisation of analytical results is a challenge. Mats contain varying levels of water; therefore, normalising toxin results to wet weight yields highly variable results, and, because mats can contain sediment, detritus, and other microbes (e.g. bacteria and fungi), normalising toxin results to dry weight can also provide misleading results. Whilst normalisation to chlorophyll-*a* eliminates many confounding components of the mats, chlorophyll-a concentrations in cyanobacteria vary with growth stage and mats will often contain other non-toxin-producing cyanobacteria and other chlorophyll-containing phytoplankton (e.g. green algae, diatoms). Normalising toxin concentrations to phycobiliproteins (phycocyanin or phycoethyrin) will be more specific to the cyanobacteria content of the mats, but as with chlorophyll-*a*, the concentration is likely to vary with growth stage and organism. For research purposes, to understand toxin production and the factors that regulate it, normalisation to the concentration of toxin-producing cells in the sample provides the most robust metric. Here, toxin concentrations are measured as an amount per toxic cell measured by droplet digital PCR (i.e. a toxin quota) and the content of

non-toxin-producing cyanobacteria, other organisms, and material is ignored (Kelly, Wood, McAllister, & Ryan, 2018; Wood & Puddick, 2017). From a risk management perspective, toxin concentrations normalised to dry weight is likely to provide the most meaningful data, as it provides an indication on the danger associated with ingesting the benthic mats by humans or animals.

Molecular tools are now routinely used to screen benthic cyanobacteria mat samples for genes involved in toxin production for both research and routine monitoring (e.g. Kelly, Bouma-Gregson, et al., 2019). Commercially available quantitative PCR kits are available and have been applied for this purpose in a number of countries (personal communication, Wood and Davis). Advancements in high-throughput sequencing have seen the widescale application of this technique to characterise the taxonomy of the cyanobacterial mat communities, this includes cyanobacteria, heterotrophic bacteria and eukaryotic algae (Echenique-Subiabre, Zancarini, et al., 2018; Pessi, Maalouf, Laughinghouse, Baurain, & Wilmotte, 2016; Zancarini et al., 2017). To date, this technique has primarily been applied for research purposes and to our knowledge is not used in any systematic monitoring programmes.

4.6 Strategies for assessing and communicating risk

Proliferations of benthic cyanobacteria in rivers, streams, lakes, and reservoirs have negative impacts on recreation and other uses such as drinking water. In lakes and reservoirs, benthic cyanobacteria can be cryptic components of the ecosystem, as they are often not visible through the water column and public awareness on their visual identification is lacking. Furthermore, blooms in rivers and streams can be overlooked as many water managers are taught to look for discoloured water as an indication of potentially toxic cyanobacterial blooms. Continued education from the research community to the water managers is needed as managers will monitor and report only what they know to look for, so it is highly likely that these events are being significantly underreported.

Benthic cyanobacterial proliferations in rivers tend to form during summer when water flows are more stable (see Introduction). This typically coincides with the time when recreational use is highest. Internationally, the human health risks posed by benthic cyanobacteria are poorly addressed in recreational guidelines, with only Cuba and New Zealand providing thresholds (Ibelings, Backer, Kardinaal, & Chorus, 2014). The New Zealand recreational cyanobacterial guidelines include a three-tier alert level framework with coverage of substrate and the occurrence of mats visibly detaching from the substrate used to determine alert level status. Although not explicitly specified in the guidelines, these alert levels were developed for *M. autumnalis* in rivers. Coverage is determined by assessing percentage cover at five points on four transects perpendicular to the river edge. The threshold levels are: *surveillance* —up to 20% coverage; *alert*— 20–50% coverage; and *action*— >50% coverage. Detached mats that accumulate along river edges are deemed high risk and automatically raise the alert level status to *action*. Monitoring and management actions are associated with each threshold, which involve changing the frequency of monitoring, cyanotoxin testing, and issuing of health warnings. The science used to develop these thresholds is preliminary and further refining will be required as knowledge and monitoring

tools improve (Wood et al., 2009). Initial steps to advance this have been undertaken but these have not resulted in any new assessment methods or guidance to date (Wood, Puddick, et al., 2018; Wood, Thomson-Laing, & Hawes, 2018).

The growth of benthic cyanobacteria in lakes and reservoirs often requires the use of underwater divers for visual monitoring of benthic cyanobacterial coverage. Although we are aware of approaches such as regular monitoring of transects for the presence of cyanobacterial mats, to our knowledge, no formal guidelines have been developed at a regional or national level.

Monitoring of large stretches of rivers or lake littoral zones is often impossible, especially given the patchy distribution and changing growth rates of mats. To overcome this, several countries have now adopted a proactive educational strategy. For example, monitoring agencies commonly use information signs to help educate the public on the appearance and risk the cyanobacteria pose, and this will allow them to make an informed decision on whether the waterbody is safe to use (e.g. https://mywaterquality.ca.gov/habs/resources/field.html#visual_guide). Mobile apps (https://cyanos.org/bloomwatch/) are also available for citizens to report the location of cyanobacterial proliferations. Because of the large spatial scales over which these proliferations occur, and their highly variable abundance, citizen science could greatly assist in documenting or highlighting problematic areas as documented recently by Valois et al. (2019).

Social media platforms (e.g. Twitter, Facebook, webpages) now play an important part in risk communication and are used to further educate the public on the risks of benthic cyanobacteria and provide information on occurrences of benthic proliferations (Wood, 2017). Other forms of communication that have been used in various countries include: information pamphlets for pet owners, text alerts that go out to registered dog owners at the start of each summer to remind them to remain vigilant at certain sites, radio and newspaper advertisements, television articles, and meetings with key stakeholders: e.g. local veterinarians and community groups.

When toxic cyanobacterial proliferations are present in drinking water supplies it may be prudent to restrict water uses and use alternative water resources. For example, many states in the U.S.A. have developed response management plans for cyanobacteria (both pelagic and benthic) (USEPA, 2019), for which closure of recreational resources is a proposed mitigation strategy. For benthic cyanobacteria, these recommendations are largely based on percent coverage of the algal proliferation and vary by jurisdiction (USEPA, 2019). Mitigation strategies include altering the depth or location of the water intake (if the infrastructure is available); a technique that has been used for pelagic cyanobacteria and would consist of a similar strategy for benthic events (USEPA, 2016). To assist with this, routine samples are collected at various depths and distances from the intake pipe (Newcombe, House, Ho, Baker, & Burch, 2010). The use of *sentinel* compounds such as odour compounds (e.g. 2-methylisoborneol) to provide warning of benthic cyanobacteria proliferations in drinking water reservoirs has proved effective in South Australia (Baker et al., 2001).

Our recommendation for communication is to ensure that pubic is educated about the risks benthic cyanobacteria pose but that this should be done in a manner that does not scare them away from using rivers or lakes. Key strategies that will help with education include the development and erection of information signs at high risk sites, the use of websites that promoting public awareness, and the development of communication strategies, which use resources available such as social media and citizen science.

5. MITIGATION

Few strategies have been employed to reduce benthic cyanobacteria. Of those applied, there is a paucity of information on how different benthic cyanobacterial species respond to each approach (Bishop & Rodgers, 2011; Calomeni, Kinley, Geer, Hendrikse, & Rodgers, 2018). Physical control typically involves mechanical removal such as hydrologic adjustments through flushing. This is a management strategy focused on altering the outflows of reservoirs to flush blooms downstream into rivers, or through in-lake hydraulic flushing. Although flushing has been studied with pelagic bloom events (Paerl, 2018), there is little information on how changing flows would impact benthic cyanobacteria communities. Flushing may be suitable for managing benthic cyanobacteria in certain circumstances, but the effectiveness may be limited due to site-specific factors (e.g. benthic proliferation size, physical catchment conditions, substrate type). This approach is expensive and requires a large amount of water, which may be limited or may directly compete with other water uses, such as drinking water and irrigation (Paerl, 2018). Consideration also needs to be given to downstream receiving environments and aquatic communities; in particular, benthic invertebrate and fish communities are likely to be severely impacted.

Below we discuss potential chemical controls; however, there are many uncertainties about the short, and long-term impacts on biodiversity and ecosystem functioning (Humbert & Quiblier, 2019). These approaches are not completely selective and, as a consequence, can have significant negative effects on aquatic ecosystems through their impact to non-target species (de Souza Beghelli, Pompêo, Rosa, & Carlos, 2016). Due to the paucity of data on long-term impacts and selectivity, these approaches should be avoided where possible. A further important caveat is that algaecides cause cells to lyse, which may result in a mass release of toxins into a waterbody. This may render the water unsafe for consumption for several weeks. The USEPA has several registered algaecides, including products based on copper, peroxide, endothall, and diquat (Calomeni et al., 2017). USEPA registered copper-based algaecides include copper sulfate, copper ethanolamine, and copper citrate/gluconate. They have been used successfully for decades to control cyanobacteria (pelagic and benthic) in lakes. Copper products act on algae by decreasing electron transport in photosystem I, preventing cell division, and inhibiting the enzyme catalase (Stauber & Florence, 1987). Several studies have shown that copper-based algaecides are successful for the control of benthic algae (Bishop, Lynch, Willis, & Cope, 2017; Bishop, Willis, & Horton, 2015; Calomeni et al., 2018). However, the efficacy of these algaecides depends on several factors, such as the formulation of copper used, initial thickness of the benthic algal mat, overall water quality, and the species composing the mat (Bishop, Richardson, & Willis, 2018; Willis, Pearce, & Bishop, 2018). Dilution and dissipation can impede the amount of copper that comes into contact with benthic cyanobacteria proliferations (Willis et al., 2018). Thus,

new application methods are being studied for increased efficacy of this compound, such as surface spray for floating mats, injection or granular application for benthic proliferations, and pulsed applications (Bishop et al., 2015; Willis et al., 2018). Due to the thick and mucilaginous structure of benthic cyanobacteria, different copper formulations have had significantly different effects on benthic proliferations. To increase efficacy, several products add surfactants (e.g. D-limonene). which degrade the mucilage and allow the copper to access and penetrate the cellular membrane. For example, Bishop et al. (2015) suggested the use of peroxides or endothall as a pre-treatment method, since these chemicals can remove organic matter surrounding the filaments, including the periphyton and mucilaginous sheath.

Peroxide-based algaecides registered through the USEPA include both liquid (hydrogen peroxide/peroxyacetic acid) and granular (sodium carbonate peroxyhydrate) formulations. Peroxide products destroy algae by forming free radicals that oxidise organic material and degrade into water and oxygen (Barroin & Feuillade, 1986). Geer, Calomeni, Kinley, Iwinski, and Rodgers (2017) demonstrated that increasing exposure of hydrogen peroxide (in the form of sodium carbonate peroxyhydrate—Phycomycin) to a benthic algal assemblage in Hartwell Lake, SC (U.S.A.) significantly reduced chlorophyll-*a* and phycocyanin concentrations by over 50%, four and seven days after treatment. However, when the benthic cyanobacteria, *M. wollei* was exposed to the same product there was no decrease in chlorophyll-*a* concentration (Calomeni, Iwinski, Kinley, McQueen, & Rodgers, 2015).Combination treatments using copper, peroxide and/or endothall products have been successful in reducing benthic cyanobacteria proliferations and may be better suited for management in the field (Calomeni et al., 2015) is a need for the greater exploration of combination chemical algaecide treatments, and the development of new products for the successful management of benthic cyanobacterial proliferations using this strategy.

One species-specific approach to consider is viral infection of cyanobacteria. Viruses are often seen in close association with cyanobacteria in their natural environment and play an important role in regulating bloom/proliferation dynamics (Wilhelm & Suttle, 1999). Approximately 25% of all virus-like particles (viruses that have not been cultured to determine host specificity) in the Gulf of Mexico are specific to the planktonic cyanobacterium *Synechococcus* (discussed in Hewson, O'Neil, & Dennison, 2001). There is limited information on viruses targeting benthic proliferations (Cheng, Frenken, Brussaard, & Van de Waal, 2019; Hewson et al., 2001; Voorhies et al., 2016). Of the few studies on benthic proliferations, Hewson et al. (2001) identified virus-like particles that were associated with a decline in *Lyngbya majuscula* Harvey ex Gomont in Moreton Bay, Australia, noting that further research was needed to understand the consequences of cyanophage-mediated collapse within these communities. Additionally, Cheng et al. (2019) assessed cyanophage infection through alterations in environmental stressors (phosphorus limitation and elevated pCO_2) in *Phormidium*. They also found that cyanophage adsorption and production rate was greater under moderate phosphorus limitation in combination with elevated pCO_2 levels, these results suggest that viral propagation and activation could increase as CO_2 levels rise. Although much work is required to transition from laboratory phase work to field applications and broaden the benthic cyanobacterial targets, viral biocontrol agents offer a promising technology for managing benthic cyanobacteria proliferations in an environmentally sustainable way.

Research on some species indicates that the greater frequency and intensity of proliferation is related to increases in nutrient and sediment inputs and habitat modification (McAllister et al., 2016; Quiblier et al., 2013). In these instances, long-term sustainable solutions are recommended. Restoring or enhancing riparian zones will provide buffers from hillslope nutrient and sediment inputs, reduce water temperatures, and increase shade (Osborne & Kovacic, 1993; Parkyn, Davies-Colley, Halliday, Costley, & Croker, 2003). These also prevent livestock access to streams and lakes, thereby reducing sediment and nutrient inputs into rivers. At a larger scale, efforts should focus on land-use within the catchment, with activities such as agriculture or forestry commonly linked to increases in sediment and nutrients (McDowell, Larned, & Houlbrooke, 2009). Habitat modification is a further consideration with flows in many streams altered, and particularly in cobble-bedded rivers near urban areas, aggregate material is often removed for building and roading, which can increase sediments loads in the short term and alter stream flows in the long term.

6. CONCLUSIONS

Reports of toxic benthic cyanobacteria continue to increase globally. This is in part due to improved monitoring and increased awareness, but in some countries and habitats there has undoubtedly been an increase in their frequency and distribution. We have identified multiple areas where future research will lead to a greater insight into the dynamic nature of benthic proliferations and toxin production and the impact on aquatic systems. Further knowledge on the causes of benthic proliferations is required to assist in developing sustainable mitigation solutions. New technologies including -omics and autonomous surveillance methods, will play a significant role. Ultimately, this new knowledge will assist in refining current monitoring, sampling, management, and mitigation options. Research in this field would be greatly expedited through the formation of international consortiums where techniques and knowledge are exchanged.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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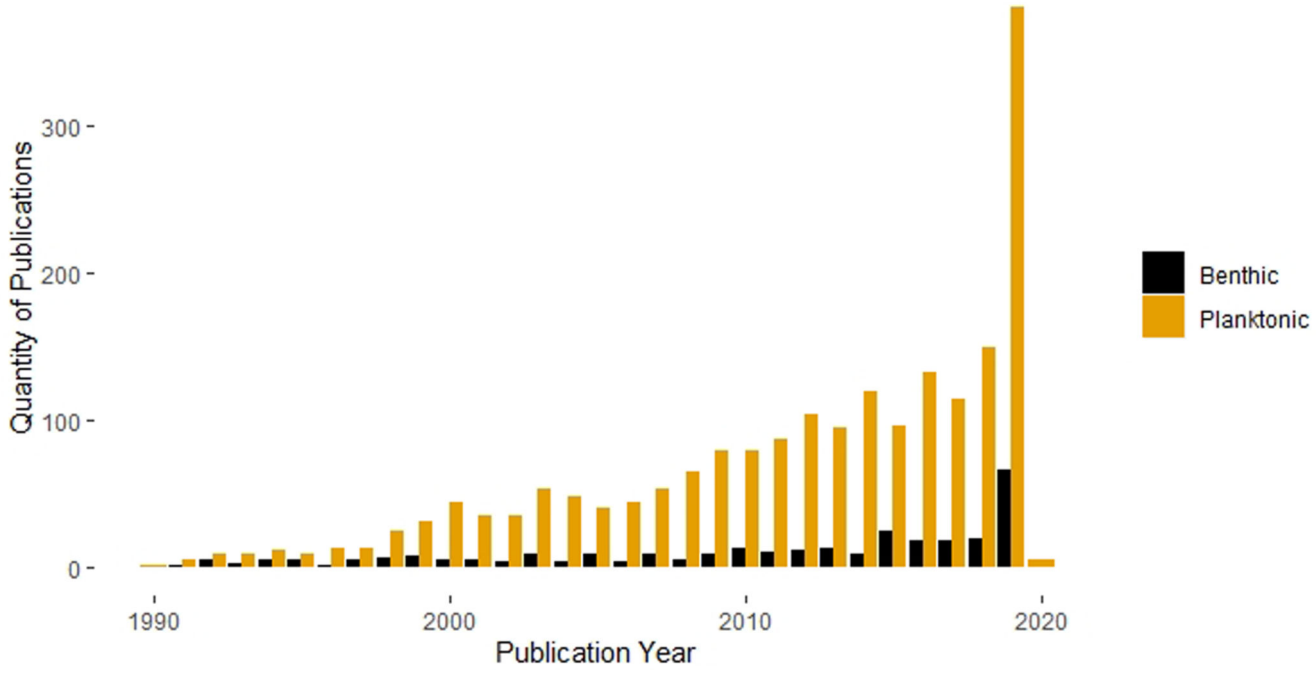

Figure 1.

Number of publications on planktonic and benthic cyanobacteria each year since 1990. These data were obtained by searching the following databases: Web of Science Core Collection, Biological Abstracts, BIOSIS Citation Index, Derwent Innovation Index, KCI-Korean Journal Database, MEDINE, Russian Science Citation Index, and SciELO Citation Index. Keywords used are given in Table S1. The search field to display was set to topic and time span was set to all years. Create marked lists (function on web of science interface) was used to exclude duplicate results

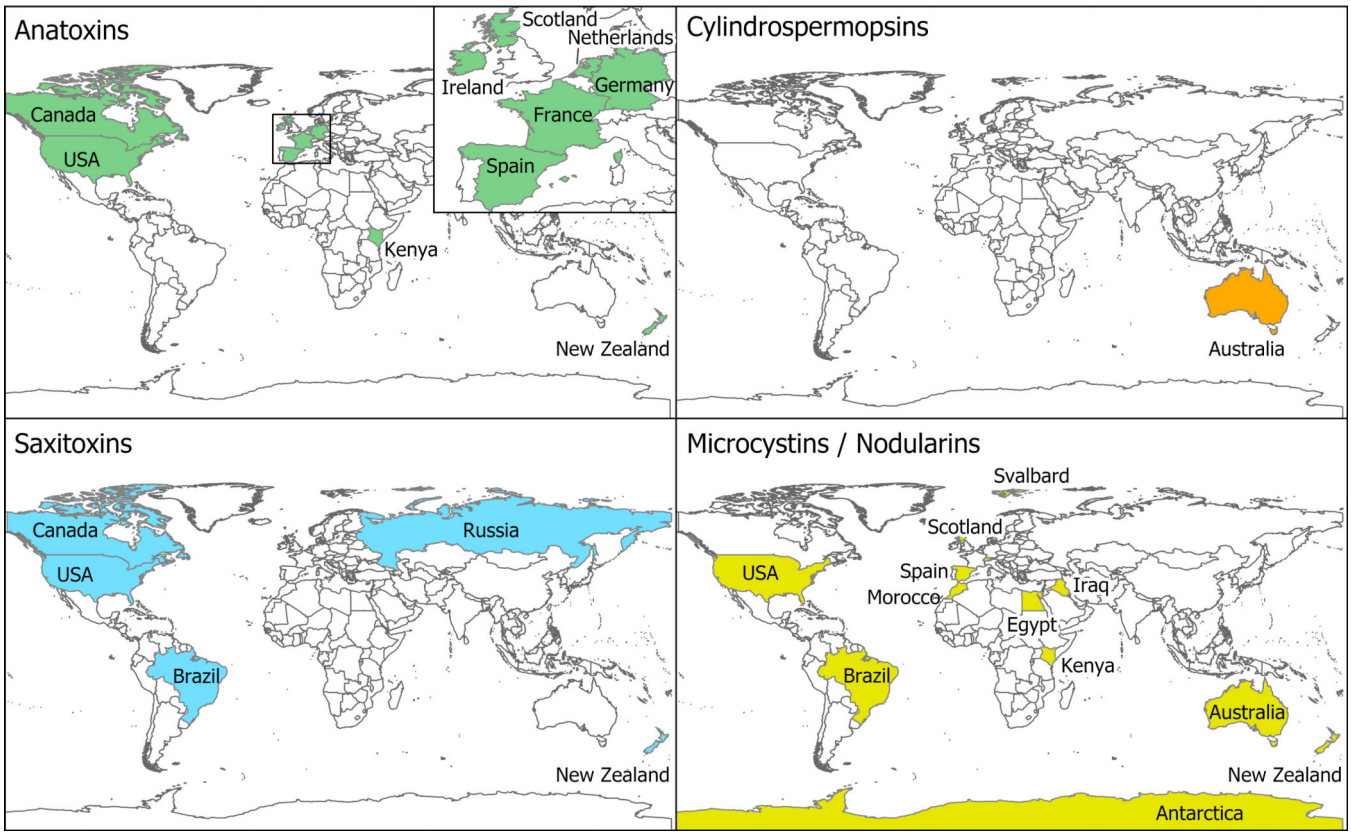

Figure 2.
Global distribution of reported cyanotoxin detections from benthic cyanobacteria

Figure 3.

Image from an unmanned aerial vehicle of the Hutt River at Upper Hutt (New Zealand) showing a proliferation of *Microcoleus autumnalis* in January 2018. Image captured with a standard red-green-blue camera

Table 1.

Global distribution of toxins associated with toxic, benthic cyanobacterial proliferations. Note that in many cases the causative producer is yet to be confirmed; i.e., further isolation and culturing are required.

Benthic cyanobacteria taxa	Habitat	Country	Screened toxins	Observed toxins	Reference
Anabaena subcylindrica, *Anabaena variabilis*, *Calothrix fusca*, *Calothrix parietina*, *Lyngbya epiphytica*, *Nostoc carneum*, *Nostoc muscorum*, *Nostoc spongiforme*, *Oscillatoria angustissima*, *Oscillatoria formosa*, *Oscillatoria granulata*, *Oscillatoria limnetica*, *Pseudanabaena catenata*, *Plectonema buryanum*, *Phormidium corium*, *Phormidium tenue*, *Rivularia bullata*, *Scytonema mirabile*, *Scytonema myochrous*	River	Egypt	MCY	MCY	Mohamed, El-Sharouny, and Ali (2006)
Anabaena, *Nostoc*, *Oscillatoria*	Lake	Russia	SXT	SXT	Belykh et al. (2016)
Aphanothece, Chroococcales	Lake	Australia	MCY	MCY	Dasey et al. (2005)
Fischerella sp.	Stream	Australia	MCY/ATX/SXT/CYN	MCY	Cirés et al. (2014)
Fischerella sp.	Dam	Brazil	MCY	MCY	Fiore et al. (2009)
Geitlerinema carotinum, *Geitlerinema splendidum*, *Phormidium uncinatum*	River, stream, and spring	Spain	MCY/ATX	MCY/ATX	Cantoral Uriza et al. (2017)
Geitlerinema lemermanii, *Geitlerinema amphibium*	Pond	Brazil	MCY/SXT	SXT	Borges et al. (2015)
Gloeotrichia natans, *Nostoc* cf. *commune*, *Oscillatoria margartifera*, *Phormidium autumnale*, *Phormidium* sp., *Pseudanabaena frigida*, *Pseudocapsa dubia*, *Rivularia biasolettiana*, *Schizothrix rivularianum*, *Scytonema drilosiphon*	River, stream, and spring	Spain	MCY/ATX	MCY	Cantoral Uriza et al. (2017)
Iningainema pulvinus	Spring	Australia	NOD	NOD	McGregor and Sendall (2017)
Leptolyngbya sp., *Microcoleus paludosus*, *Cyanothece* sp., *Phormidium murrayi*, *Nostoc* sp., *Calothrix* sp.	Lake	New Zealand	ATX/HTX/MCY/NOD	NOD	Wood, Kuhajek, de Winton, and Phillips (2012)
Microcoleus autumnalis	River	New Zealand	ATX/HTX/CYN/MCY/SXT	ATX/HTX	Heath et al. (2010), Heath et al. (2011); Wood et al. (2007)
Microcoleus autumnalis	Rivers	U.S.A.	ATX/HTX	ATX	Bouma-Gregson et al. (2018); Bouma-Gregson et al. (2019)
Microcoleus autumnalis	Rivers	U.S.A.	ATX/dhATX/HTX/dhHTX/MCY/NOD/CYN	ATX/dhATX/HTX	Kelly, Bouma-Gregson, et al. (2019)
Microseira wollei	River	Australia	CYN/ATX/SXT/LTX/MCY/ApTX	CYN	Seifert et al. (2007)

Benthic cyanobacteria taxa	Habitat	Country	Screened toxins	Observed toxins	Reference
Microseira wollei	River	Canada	ATX/NOD/MCY/SXT/CYN	SXT	Lajeunesse et al. (2012)
Microseira wollei	Lake	U.S.A.	SXT/ MCY/ATX/CYN	STX/ATX	Smith et al. (2019)
Microseira wollei	Reservoir	U.S.A.	SXT	SXT	Carmichael, Evans, Yin, Bell, and Moczydlowski (1997)
Microseira wollei	Springs	U.S.A.	SXT	SXT	Foss, Phlips, Yilmaz, and Chapman (2012)
Mixed species mats		Antarctica/Arctic	MCY	MCY	Kleinteich et al. (2012)
Nostoc sp.	Lake	Brazil	NOD	NOD	Jokela et al. (2017)
Nostoc sp.	Lake	New Zealand	MCY/SXT	MCY	Wood et al. (2006)
Nostoc linckia, *Limnothrix mirabilis*	Reservoir	Australia	MCY	MCY	Gaget, Humpage, Huang, Monis, and Brookes (2017)
Nostoc muscorum, *Oscillatoria*, *Pseudanabaena*	River	Morocco	MCY	MCY	Oudra, Dadi-El Andaloussi, and Vasconcelos (2009)
Nostoc sp.		Antarctica	MCY	MCY	Wood et al. (2008)
Oscillatoria sp.	Lake	Ireland	ATX	ATX	James, Sherlock, and Stack (1997)
Oscillatoria sp.	Lake	Scotland	ATX	ATX	Edwards et al. (1992)
Oscillatoria limosa, *Phormidium konstantinosum*	Lake	Switzerland	ii	MCY	Mez et al. (1997)
Oscillatoriaceae?	River	U.S.A., Ontario	ATX	ATX	Puschner et al. (2008)
Oscillatoriales	Lake	U.S.A.	MCY	MCY	Izaguirre, Jungblut, and Neilan (2007)
Oscillatoria-like genus	River	New Zealand	ATX/MCYs/ STX	ATX	Hamill (2001)
Phormidium ambiguum	Reservoir	Australia	CYN/deoxy-CYN	CYN/deoxy-CYN	Gaget et al. (2017)
Phormidium favosum	River	France	MCY/SXT/ATX	ATX	Gugger et al. (2005)
Phormidium favosum, *P. amoenum*	Reservoir	Australia	Mouse bioassay	nd	Baker et al. (2001)
Phormidium or *Oscillatoria* sp.	River	New Zealand	ATX/MCY/SXT	MCY	Wood et al. (2006)
Phormidium sp.	River	France	ATX/HTX	ATX/HTX	Cadel-Six et al. (2007)
Phormidium sp.	Lake	Netherlands	ATX/HTX/CYN/SXT	ATX/HTX	Faassen et al. (2012)
Phormidium sp.	Lake	U.S.A.	MCY	MCY	Shishido et al. (2019)
Phormidium sp., *Oscillatoria* sp., *Lyngbya* sp., *Tolypothrix distorta*, *Calothrix parietina*, *Rivularia biasolettiana*	Reservoir	Spain	MCY	MCY	Aboal and Puig (2005)
Phormidium terebriformis, *Oscillatoria willei*, *Spirulina subsalsa*, *Synechococcus bigranulatus*	Hot spring	Kenya	MCY/ATX	MCY/ATX	Krienitz et al. (2003)

Freshw Biol. Author manuscript; available in PMC 2021 December 29.

Benthic cyanobacteria taxa	Habitat	Country	Screened toxins	Observed toxins	Reference
Phormidium uncinatum	River	France	ATX/MCY/SXT	ATX	Echenique-Subiabre, Tenon, et al. (2018); Echenique-Subiabre, Zancarini, et al. (2018)
Phormidium uncinatum, *Pseudanabaena catenata*, *Cylindrospermum stagnale*	River, stream, and spring	Brazil	SXT/MCY	SXT/MCY	Borges et al. (2015)
Phormidium, *Oscillatoria*, *Lyngbya*, *Nostoc*, *Nodularia*, *Anabaena*	Meltwater pond	Antarctica	MCY	MCY	Jungblut et al. (2006)
Planktothrix sp.	River	New Zealand	ATX/HTX/MCY/CYN/NOD/STX	MCY	Wood, Heath, Holland, et al. (2010)
Rivularia spp., *Schizothrix fasciculata*, *Tolypothrix distorta*, *Phormidium splendidum*	River	Spain	MCY	MCY	Aboal, Puig, and Asencio (2005)
Schizothrix lateritia, *Phormidium fragile*, *Phormidium oveolarum*, *Pleurocapsa minor*, *Calothrix parietina*, *Tolypothrix distorta*	River	Spain	Microtox method	Yes (nd)	Aboal, Puig, Mateo, and Perona (2002)
Scytonema sp.	Reservoir	New Zealand	SXT	SXT	Smith, Wood, van Ginkel, Broady, and Gaw (2011)
Tychonema sp.	Lake	Germany	MCY/CYN/ATX/HTX/dhATX/dhHTX	ATX/dhATX	Fastner et al. (2018)
Unidentified	Streams	U.S.A.	NOD/MCY	NOD/MCY	Foss et al. (2017)
Unidentified	Streams	U.S.A.	MCY/SXT/ATX/LTX	MCY/SXT/ATX/LTX	Fetscher et al. (2015)

Abbreviations: ATX, anatoxin-a; CYN, cylindrospermopsins; dhATX, dihydroanatoxin-a; dhHTX, dihydrohomoanatoxin-a; HTX, homoanatoxin-a; ii, insufficient information; LTX, lyngbyatoxins.; MCY, microcystins; nd, not determined; NOD, nodularins; SXT, saxitoxins.