



REPORT NO. 3765

**CLIMATE CHANGE AND TOXIC FRESHWATER  
CYANOBACTERIA IN AOTEAROA NEW ZEALAND**

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# CLIMATE CHANGE AND TOXIC FRESHWATER CYANOBACTERIA IN AOTEAROA NEW ZEALAND

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Prepared for the New Zealand Ministry of Health

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## EXECUTIVE SUMMARY

Climate change is already impacting freshwaters in Aotearoa New Zealand. Water temperatures are rising, rainfall and snowfall patterns are changing, and the frequency of extreme weather events is increasing. These changes are having a profound effect on the physical and chemical conditions of freshwaters, and direct and indirect impacts on our flora and fauna.

Cyanobacteria, or blue-green algae, are expected to flourish with continued climate change. Many cyanobacteria species produce toxins that pose a health risk to animals and humans through physical contact, or by consuming them via contaminated water or aquatic foodstuffs. The Ministry of Health commissioned the Cawthron Institute to review how climate change will likely affect problematic cyanobacteria in Aotearoa New Zealand and how these changes could impact human health.

Our review of the international literature provided compelling evidence that planktonic cyanobacteria in lakes and reservoirs will increase. The type of changes will vary with region but will include more intensive blooms of longer duration, blooms in a greater number of lakes, and changes in dominant species. There is less consensus on how climate change will impact cyanotoxin production, with studies exploring parameters such as temperature and pH showing contrasting results. There is some evidence that temperature will increase the growth rates of benthic cyanobacteria. However, international data on the effect of climate change on benthic cyanobacteria are very limited.

Based on published data, we predict that the intensity, duration, and distribution of planktonic cyanobacterial blooms in lakes and reservoirs, and benthic proliferations in rivers, streams and lakes in Aotearoa New Zealand will increase with climate change. However, only a few studies have directly explored the likely impacts of climate change on cyanobacteria in Aotearoa New Zealand. Modelling studies provide clear evidence that changes in internal nutrient loading will favour cyanobacteria in some lakes. A 17-month study of a eutrophic lake highlighted the complexity of predicting the impacts of climate change on key bloom-forming genera, with complex species shifts occurring in response to nutrient dynamics related to extreme climate events. Whilst much of the research conducted on the drivers of benthic proliferations in rivers and streams has been undertaken in Aotearoa New Zealand, it has not focused specifically on climate change. Several field studies across multiple years and rivers highlight the importance of river flow and temperature in regulating proliferations—climate change is expected to impact both of these parameters. Benthic toxin-producing cyanobacteria also occur in lakes in Aotearoa New Zealand, but there are insufficient data to predict how climate change will impact their abundance. Multiple studies have shown that cyanotoxins can accumulate in aquatic food found in this country, including kākahi (freshwater mussels), kōura (freshwater crayfish), tuna (eels) and trout. Consumption of contaminated organisms poses a potential health risk to humans that will likely increase with climate change.

The review highlighted a need for more knowledge on:

- the current distribution, taxonomy and toxin content of planktonic and benthic cyanobacteria in lakes, reservoirs, rivers and streams;
- how extreme weather events, in particular storms and droughts, will affect cyanobacterial species in lakes, rivers, and streams; and
- the accumulation of cyanotoxins in a wider range of aquatic organisms.

There is also a need to enhance our ability to predict how benthic cyanobacteria will respond to climate change and to improve cyanobacterial monitoring programmes so that they capitalise on new technology.

Based on the findings of this review, we anticipate that continued climate change will increase the likelihood of people in Aotearoa New Zealand being exposed to cyanotoxins. The main routes of exposure will be during recreational activities (accidental consumption of water and aerosols), from drinking-water (when there is inadequate water treatment undertaken), and via the consumption of aquatic foodstuffs sourced from contaminated water bodies. Continued and improved risk minimisation strategies, including public education initiatives will help to limit this exposure.

The impacts of climate change will be further compounded by the intensification of other stressors on lakes, rivers and streams, for example, ongoing eutrophication and the introduction of non-native species. All efforts aimed at improving the health of waterways are, therefore, also expected to lessen the likelihood of increased cyanobacterial abundance in waterbodies around Aotearoa New Zealand.

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## GLOSSARY

Adda	A unique amino acid found in microcystins and nodularins (3-amino-9-methoxy-2,6,8-trimethyl-10-phenyldeca-4,6-dienoic acid).
ALS-PDC	Amyotrophic lateral sclerosis and Parkinsonism–dementia complex.
Benthic cyanobacteria	Cyanobacteria that grow attached to a substrate (e.g., on the bottom of a lake or river).
BMAA	$\beta$ -methylamino-alanine.
CO <sub>2</sub>	Carbon dioxide.
Diazotrophic	Capable of fixing atmospheric nitrogen.
DIC	Dissolved inorganic carbon.
DYRESM-CAEDYM	Dynamic reservoir simulation model - Computational aquatic ecosystem dynamics model (a one-dimensional hydrodynamic-ecological model for lakes and reservoirs).
ELISA	Enzyme-linked immunoassay.
GAMMs	Generalised additive mixed models (linear modelling approach).
LPS	Lipopolysaccharide.
LC-MS	Liquid chromatography-mass spectrometry.
Mahinga kai	A Māori term for gathered food, the practice of gathering food from the wild or a location where food is gathered from (a food bowl).
MfE	Ministry for the Environment.
MoH	Ministry of Health.
Planktonic cyanobacteria	Cyanobacteria that grow free-floating in the water column.
SAWT	Soil and water assessment tool (small watershed to river basin-scale model).



# 1. GENERAL INTRODUCTION

Changes in the climate of Aotearoa New Zealand have already been observed and will likely continue to intensify in the coming decades (IPCC Working Group II 2022). Climate change is expected to change the amount and distribution of rainfall and snowfall, which will affect the quantity of water in our rivers, streams, lakes and groundwater systems. The frequency of extreme weather events is also expected to increase, causing greater nutrient and sediment inputs into our freshwaters. Rising temperatures will have profound effects on our freshwater systems, impacting our flora, fauna and the physical environment. For example, some species will flourish in warmer waters, while others will no longer survive, and warmer temperatures will cause some lakes to stratify for longer with flow on impacts on nutrient cycling and dissolved oxygen dynamics.

Cyanobacteria, also known as blue-green algae, are regarded globally as organisms that will flourish as climate change continues (O'Neil et al. 2012). Cyanobacteria thrive in warm, nutrient rich waters and are highly adaptive to changing nutrient regimes and physical conditions. It is anticipated that cyanobacteria blooms and benthic proliferations will increase in intensity, distribution, and duration, impacting the health of our aquatic ecosystems. Because many species produce toxic compounds, these shifts pose an increased risk to the health of human and animals.

The Ministry of Health (MoH) commissioned the Cawthron Institute (Cawthron) to review how climate change will likely impact problematic cyanobacteria in Aotearoa New Zealand and how these changes could affect human health. This report provides:

- an overview of cyanobacteria, their toxins and negative impacts on ecosystems and human health, with a focus on issues specific to Aotearoa New Zealand
- a review of global research which focuses on how cyanobacteria will respond to climate change
- a review of global research on how cyanotoxin production will change under predicted climate change scenarios
- an overview of how climate change will impact lakes, rivers and streams in Aotearoa New Zealand, and how this will likely affect the distribution and abundance of cyanobacteria and cyanotoxins. As part of this section, we review research undertaken in Aotearoa New Zealand that provides insights into the likely responses of cyanobacteria to climate change.
- a review of the potential public health risks in Aotearoa New Zealand in response to predicted changes in cyanobacteria and their toxins
- a synthesis of knowledge gaps related to climate change and cyanobacteria, their toxins and human health risks.

## 2. CYANOBACTERIA, THEIR TOXINS AND IMPACTS ON HUMANS AND ECOSYSTEMS

### 2.1. Cyanobacteria and problematic taxa in Aotearoa New Zealand

Cyanobacteria, also known as blue-green algae, are photosynthetic prokaryotic organisms found in a diverse range of ecosystems including oceans, freshwaters, bare rock, thermal springs and soil (Whitton 2012). In freshwater aquatic ecosystems, when hydrological and / or environmental conditions are favourable, cyanobacteria cells can multiply and form planktonic (free-floating) blooms or benthic (attached to substrates) proliferations. These blooms / proliferations are aesthetically unpleasant and can cause a suite of water quality issues, such as low dissolved oxygen in ponds and lakes, which can ultimately lead to fish deaths and other flow-on impacts on the ecosystem (discussed further in Section 1.3; see also Robarts et al. 2005; Havens 2008).

Additionally, some cyanobacterial species produce natural toxins collectively known as cyanotoxins. These natural toxins are a threat to humans and animals when consumed or through contact with them (Wood & Smith 2006). The toxicity mechanisms for cyanotoxins are very diverse, ranging from hepatotoxicity and neurotoxicity, to dermatotoxicity. Based on their chemical structure, cyanotoxins can be divided into four broad groups; alkaloids (cylindrospermopsins, anatoxins and saxitoxins), amino acids ( $\beta$ -methylamino-alanine), cyclic peptides (microcystins and nodularins) and lipopolysaccharides (LPS). A more detailed description of each cyanotoxin is provided in Section 2.4.1.

Table 1. Cyanotoxins produced by freshwater cyanobacteria. Adapted from Table 3.1 of Chorus & Bartram (1999).

Cyanotoxin	Primary Target in Mammals	Structural Characteristics
Anatoxin-a	Nerve synapse – Agonists of nicotinic acetylcholine receptors	Bicyclic secondary amine
Anatoxin-a(S)	Nerve synapse – Acetylcholinesterase inhibitors	Organophosphate alkaloid
Cylindrospermopsins	Liver – Protein synthesis inhibitors	Tricyclic alkaloid with attached uracil
Saxitoxins	Nerve axon – Blockage of voltage-gated sodium channels	Tricyclic alkaloid
Microcystins	Liver – Protein phosphatase inhibitors	Cyclic heptapeptide
Nodularins	Liver – Protein phosphatase inhibitors	Cyclic pentapeptide
$\beta$ -methylamino-alanine	Unknown – Thought to lead to neurodegenerative diseases	Non-proteinogenic amino acid
Lipopolysaccharides	Dermis – Irritant of all exposed tissue	Lipopolysaccharide

## 2.2. Planktonic cyanobacterial blooms in Aotearoa New Zealand

Cyanobacterial blooms have been a regular occurrence in some lakes in Aotearoa New Zealand since the 1970s (MfE & MoH 2009). However, they have become increasingly prominent in recent decades. The most common bloom-forming cyanobacterial genera are *Microcystis* and *Dolichospermum* (Figure 1A/B). *Raphidiopsis raciborskii* (previously *Cylindrospermopsis raciborskii*; Figure 1C) can also form extremely dense blooms in Waikato lakes (Wood et al. 2014a) and *Nodularia spumigena* blooms are frequently reported in brackish water lakes (Dolamore et al. 2017). Blooms of *Aphanizomenon* sp. and *Cuspidothrix issatschenkoi* are also reported, albeit less frequently (Wood et al. 2007a). More detail on some of these genera are provided below.

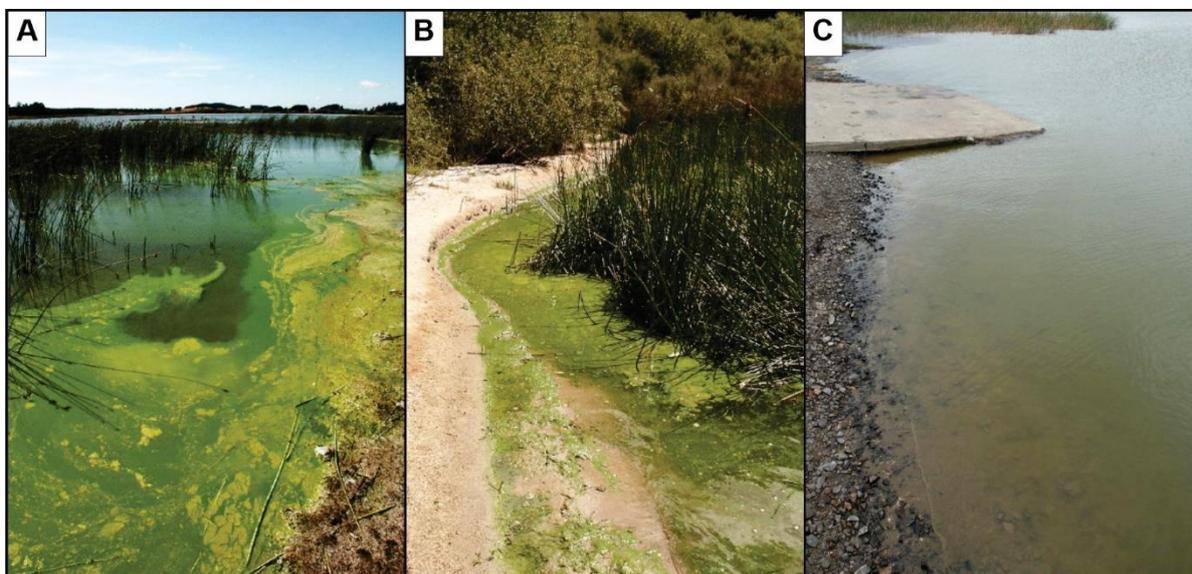


Figure 1. Examples of planktonic cyanobacterial blooms from Aotearoa New Zealand. **A)** *Microcystis* sp. (Lake Horowhenua, Levin), **B)** a mixture of *Dolichospermum lemmermannii* and *Microcystis* sp. (Lake Rotoehu, Rotorua region), and **C)** *Raphidiopsis raciborskii* (Lake Waahi, Waikato region).

Prior to 1987, 33 lakes in Aotearoa New Zealand were recorded as having experienced cyanobacterial blooms. A survey in 2005 added an additional 18 lakes to this (Wood 2004). We anticipate that this number is now much higher, but neither a formal collation of available data from regional councils nor a survey measuring cyanobacterial biomass in lakes has been undertaken in the last decade. Recent spatial modelling undertaken by the Ministry for the Environment (MfE) predicts that 46% of Aotearoa New Zealand's lakes (approx. 1,750 lakes) are in a eutrophic condition or worse (MfE & Stats NZ 2022). It is highly likely that lakes in a eutrophic condition will experience cyanobacterial blooms, particularly during summer months (Wood et al. 2016a). This suggests that cyanobacterial blooms are a major issue

impacting lakes in Aotearoa New Zealand. Planktonic cyanobacteria in Aotearoa New Zealand are known to produce anatoxin-a, cylindrospermopsins, microcystins and nodularins (Table 2).

Table 2. Summary of known toxin-producing cyanobacterial species in Aotearoa New Zealand. Benthic species are in bold type.

Cyanobacteria genus / species	Cyanotoxin	Reference/s
<i>Cuspidothrix issatschenkoi</i> (previously <i>Aphanizomenon issatschenkoi</i> )	Anatoxin-a	Wood et al. (2007a)
<i>Raphidiopsis raciborskii</i> (previously <i>Cylindrospermopsis raciborskii</i> )	Cylindrospermopsin*, deoxycylindrospermopsin*	Stirling & Quilliam (2001) Wood & Stirling (2003)
<i>Microcystis</i> spp.	Microcystins	Wood et al. (2005)
<i>Nodularia spumigena</i>	Nodularin	Carmichael et al. (1988)
<b><i>Nostoc</i> sp.</b>	Microcystins	Puddick et al. (2019)
<b><i>Oscillatoria</i> sp.</b>	Anatoxins*, microcystins*	Hamill (2001)
<b><i>Microcoleus autumnalis</i></b> (previously <i>Phormidium autumnale</i> )	Anatoxins	Wood et al. (2007b) Heath & Wood (2010)
<b><i>Planktothrix</i> sp.</b>	Microcystins	Wood et al. (2010a)
<b><i>Scytonema</i> cf. <i>crispum</i></b>	Saxitoxins	Smith et al. (2011)

\* = Observations were made using environmental material rather than cultured cyanobacterial strains. *Dolichospermum lemmermannii* may produce anatoxin-a\* (Wood et al. 2006b), but this result is based off analysis of a single environmental sample. *Dolichospermum planctonicum* may produce saxitoxins\* based on low level positives from analysis of environmental samples using ELISA (Kouzminov et al. 2007), but this result has not been confirmed using robust analytical methods.

### 2.2.1. Common bloom-forming planktonic cyanobacteria in Aotearoa New Zealand

Below is a summary of general information on bloom-forming cyanobacteria observed in lakes around Aotearoa New Zealand. This content has been adapted from Wood et al. (2015b) and Kelly et al. (2021).

#### ***Dolichospermum***

*Dolichospermum* (formally known as *Anabaena*) is a ubiquitous filamentous diazotrophic genus found worldwide. Globally, species within this genus have been reported to produce an array of cyanotoxins including; microcystins, anatoxin-a, cylindrospermopsin, guanitoxin / anatoxin-a(S) and saxitoxin (Chorus & Welker 2021). Using molecular techniques, researchers have shown that field populations of *Dolichospermum* comprise both toxic and non-toxic strains (Vaitomaa et al. 2003). To date, no toxin-producing *Dolichospermum* strains have been isolated in New Zealand.

### ***Microcystis***

*Microcystis* is a ubiquitous cyanobacterial genus that has been identified on all continents except Antarctica (Harke et al. 2016). *Microcystis* is well known as a bloom-forming cyanobacterial genera and is commonly associated with the production of microcystins. Both toxic and non-toxic genotypes of *Microcystis* exist and both are usually present in a bloom but cannot be distinguished microscopically. Molecular analysis for microcystin synthase genes (Tillett et al. 2000) or analysis for the toxins themselves (Hawkins et al. 2005) is required to determine if toxin-producing genotypes are present. *Microcystis* can regulate its buoyancy and position in the water column through gas vesicle production to become positively buoyant (Walsby 1975, 1994) and through carbohydrate stores to become negatively buoyant (Visser et al. 1995; Visser et al. 1997). *Microcystis* is the most prevalent microcystin-producing cyanobacterial genera in Aotearoa New Zealand (Puddick et al. 2019).

### ***Nodularia***

*Nodularia spumigena* is a diazotrophic cyanobacterium found in brackish waters worldwide. It is well known as the most common producer of nodularins, a class of hepatotoxins structurally similar to microcystins. In Aotearoa New Zealand, *Nodularia spumigena* blooms have been reported from Wairewa (Lake Forsyth) and Waihora (Lake Ellesmere; both in the Canterbury region) since the 1970s, with corresponding stock deaths recorded (Conner 1977). Nodularin-producing *Nodularia spumigena* is also present in Whakakā Lake (Hawkes Bay region; Puddick et al. 2022).

### ***Raphidiopsis***

*Raphidiopsis raciborskii* is a solitary, filamentous diazotrophic freshwater cyanobacterium. It was initially believed to be confined to tropical environments, but over the past few decades appears to have expanded its range to many temperate regions across the globe (Padisák 1997; Hamilton et al. 2005; Wood et al. 2014a). In New Zealand, cylindrospermopsin-producing *R. raciborskii* has been detected once from Lake Waahi (Wood & Stirling 2003). Although *R. raciborskii* is commonly found in lakes in the Waikato region, no further reports of cylindrospermopsin production have been recorded.

## **2.3. Benthic cyanobacterial proliferations in Aotearoa New Zealand**

### ***2.3.1. Rivers and streams***

Benthic, mat-forming cyanobacteria are widespread throughout New Zealand rivers and streams and are found in a wide range of water-quality conditions, including those with very good water quality (Biggs & Kilroy 2000). Benthic proliferations (defined in this report as > 20% coverage of the river / stream substrate) generally only occur in rivers where there is some at least moderate level of degradation; e.g., increased nitrogen or sediment loads. The most common mat-forming species in New Zealand that forms proliferations is *Microcoleus autumnalis* (previously *Phormidium*

*autumnale*). During stable flow conditions *Microcoleus* mats can proliferate, at times forming expansive black-brown leathery mats across large expanses of river and stream substrate (Figure 2). In Aotearoa New Zealand, dog deaths associated with *Microcoleus* mats in rivers have become more common over the past two decades (Hamill 2001; Wood et al. 2007b). In most instances these deaths have been associated with the presence of the neurotoxins, known as anatoxins, produced by *Microcoleus* (Wood et al. 2007b). Whilst there have been anecdotal reports of humans becoming sick after swimming in rivers and streams with extensive *Microcoleus* mats, there is a lack of conclusive evidence that anatoxins were the cause (personal knowledge of Susie Wood).

A review undertaken in 2016 collated records of rivers and streams that had experienced *Microcoleus* proliferations (McAllister et al. 2016). The authors identified that *Microcoleus* proliferations had occurred at one or more sites in 103 rivers and streams across Aotearoa New Zealand since 2009 (61 rivers/streams in the North Island and 42 rivers / streams in the South Island). In general, the rivers and streams with proliferations tended to be on the eastern side of the country, often in the rain shadow of prevailing westerly winds.

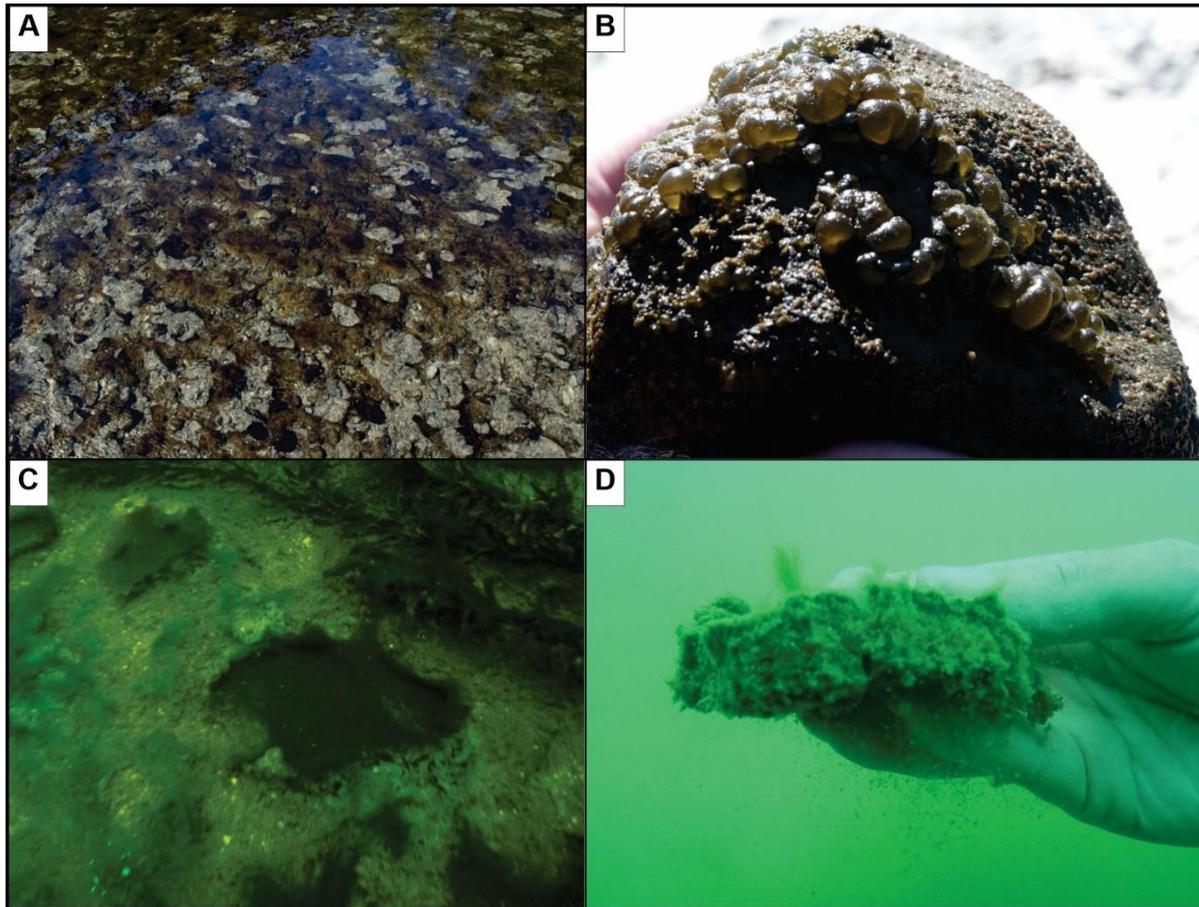


Figure 2. Examples of benthic cyanobacterial proliferations from Aotearoa New Zealand. **A)** *Microcoleus* mats in the Waipoua River (North Island, New Zealand, **B)** *Nostoc* mats from Lake Taupō, **C)** Benthic mats in Lake Rotoiti (Rotorua region), and **D)** Lake Tikitapu (Rotorua region). Photographers: Top row, Susie Wood (Cawthron Institute, New Zealand); bottom row, Rohan Wells (National Institute of Water and Atmospheric Research, New Zealand).

Proliferation of other species are reported, albeit less frequently. The production of microcystins by benthic cyanobacteria in rivers and streams (*Nostoc* sp. and *Planktothrix* sp.) has been observed in New Zealand (Wood et al. 2006b; Wood et al. 2010a; Puddick et al. 2019) and in at least one instance a dog death was caused by microcystins (Wood et al. 2010a). Microcystins / nodularins were also detected (via Adda-ELISA) in benthic *Oscillatoria* mats from the Mataura River (Hamill 2001).

Known benthic toxin producers in Aotearoa New Zealand are given in bold text in Table 2 (see Section 2.2).

### 2.3.2. Lakes, reservoirs and ponds

Proliferations of benthic cyanobacteria are likely relatively common in lakes, reservoirs and ponds across Aotearoa New Zealand; however, very little is known about their taxonomy, ecology, abundance or distribution. Unlike planktonic blooms, which

generally occur in lakes with elevated nutrients, benthic proliferation can occur in lakes with good water quality. The stable substrate in lakes give the mats ample time to proliferate and, once the mats start to form, a suite of microbial and geochemical processes occurs within the mats (Wood et al. 2015a; Tee et al. 2020). These strategies mean that their growth is not limited by the nutrients in the water column. Wood et al. (2012b) studied the abundance, taxonomy and toxin content of three Te Arawa lakes (Rotorua region), each with a different trophic status; Tikitapu (oligotrophic), Ōkāreka (mesotrophic) and Rotoiti (eutrophic). In specific regions of each lake, cyanobacterial mats were abundant (Figure 2C and D), with molecular analysis indicating that the dominant taxa in the mats from Rotoiti and Ōkāreka were most similar to *Phormidium* and *Oscillatoria*, whereas those from Tikitapu showed low sequence similarity to other molecularly characterised cyanobacteria. Cyanotoxin analysis identified nodularin in all mats from Lake Tikitapu, although, the causative producer could not be identified.

Benthic mats composed of *Nostoc* are often observed in clear water lakes with rocky substrates. A sample collected from the eastern shoreline of Lake Taupō in 2003 (Figure 2) contained high levels of a range of microcystins (Wood et al. 2006b). Although more commonly associated with rivers and streams, proliferations of *Microcoleus* can also occur in lentic habitats (lakes, ponds and reservoirs). In 2014, detached *Microcoleus* mats containing a high level of anatoxins were responsible for a dog death at a farm pond in Kaikōura (Wood et al. 2016b).

Saxitoxins have been identified in benthic *Scytonema* found in a range of lakes with variable water source and trophic status in the South Island (Smith et al. 2011, 2012). Unlike many other benthic cyanobacteria, *Scytonema* in these lakes grows amongst the reeds and macrophytes and could easily be misidentified.

Known benthic cyanotoxin producers in Aotearoa New Zealand are provided in bold text in Table 2 (see Section 2.2).

## 2.4. Negative effects from cyanobacteria

### 2.4.1. Cyanotoxins

There are approximately 2,000 cyanobacteria species described worldwide and more than 50 are known to have strains which produce natural compounds which are toxic (cyanotoxins).

#### **Anatoxins**

Anatoxins are alkaloid toxins (Figure 3A) that block neuromuscular signalling through the nicotinic acetylcholine receptor (Carmichael & An 1999). The toxins induce convulsions, coma, rigors, cyanosis, limb twitching, hypersalivation and death in animals exposed to sufficiently high levels. Whilst the toxins have been linked with

animal and wildfowl poisonings, there have been no sufficiently verified reports of human poisonings / fatalities from anatoxins (Ressom et al. 1994).

#### **Anatoxin-a(S) / Guanitoxin**

Anatoxin-a(S) (Figure 3B) was recently renamed guanitoxin in order to avoid confusion with the structurally dissimilar anatoxin-a (Fiore et al. 2020b). This cholinesterase inhibitor induces hypersalivation, diarrhoea, shaking and nasal mucus discharge in mammals (Mahmood & Carmichael 1987; Carmichael 1992). Guanitoxin / anatoxin-a(S) was originally identified in *Dolichospermum lemmermannii* (Henriksen et al. 1997) and *Dolichospermum flos-aquae* (Mahmood & Carmichael 1987), but has recently also been identified in *Sphaerospermopsis torques-reginae* (Fernandes et al. 2020, 2021; Lima et al. 2022). Because it is so rarely detected, very little research has been undertaken on this toxin so it is not discussed further throughout this report.

To the best of our knowledge, no studies specifically analysing for guanitoxin / anatoxin-a(S) have been conducted in Aotearoa New Zealand. The primary reason is that no commercial standards are available for the toxin, limiting the ability to set up robust detection methods here. The recent identification of guanitoxin / anatoxin-a(S) in *Sphaerospermopsis torques-reginae* and the associated characterisation of the biosynthetic pathway for the toxin (Lima et al. 2022) may lead to future opportunities to understand the prevalence and distribution of this under-researched cyanotoxin. The reliable production of guanitoxin / anatoxin-a(S) from *Sphaerospermopsis torques-reginae* (Fernandes et al. 2020, 2021) may also lead to standards for the toxin becoming available, allowing detection by analytical methodologies.

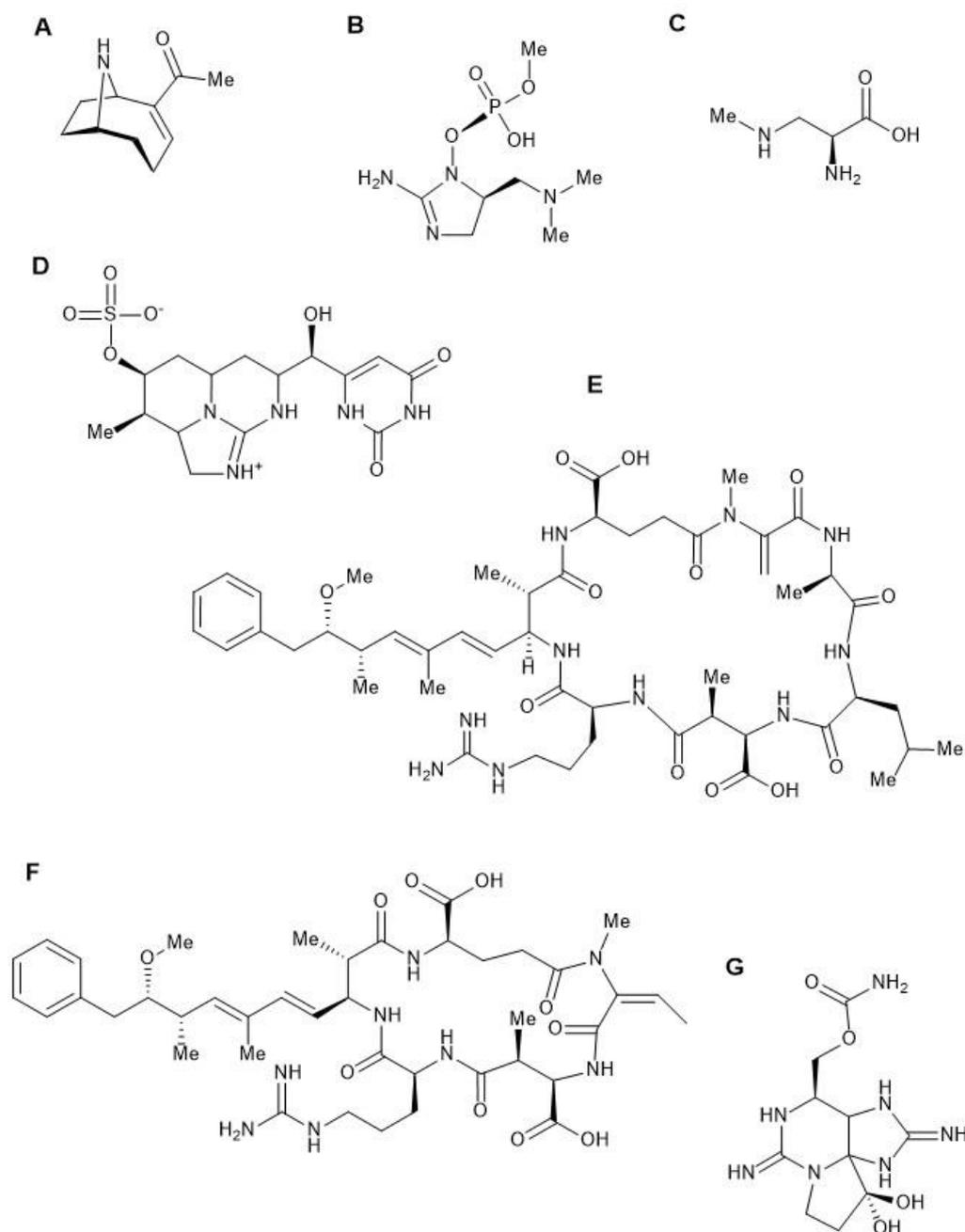


Figure 3. Chemical structures of several common freshwater cyanotoxins. **A)** anatoxin-a, **B)** anatoxin-a(S) / guanitoxin, **C)**  $\beta$ -methylaminoalanine, **D)** cylindrospermopsin, **E)** microcystin-LR, **F)** nodularin-R and **G)** saxitoxin.

### $\beta$ -methylaminoalanine

$\beta$ -methylaminoalanine (BMAA; Figure 3C) is a non-proteinogenic amino acid that has been observed in some cyanobacteria (e.g., certain *Nostoc* species). BMAA is considered a possible cause of neurodegenerative disorders such as amyotrophic lateral sclerosis and Parkinsonism–dementia complex (ALS-PDC). The connection was first made among the Chamorro people of Guam who had extremely high rates of incidence of ALS-PDC. This was linked to the BMAA produced by *Nostoc*

(cyanobacteria) growing as a symbiont on cycad trees and biomagnifying through the food chain. In this instance, the Chamorro people ate fruit bats which feed on cycad seeds that contain BMAA from the symbiotic *Nostoc* (Cox & Sacks 2002; Cox et al. 2003). The potential link between cyanobacteria and neurodegenerative disorders is also supported by epidemiological studies that have identified higher rates of neurodegenerative disorders in people living close to lakes or associating with lakes more frequently (Sienko et al. 1990; Caller et al. 2009, 2012; Andrew et al. 2017; Fiore et al. 2020a). Because of discrepancies in the specificity of analytical methodologies used by different research groups, it is currently not clear how widespread BMMA production in cyanobacteria is. A strong toxicological link between BMAA and neurodegenerative disorders has also not yet been established (Chorus & Welker 2021). For these reasons, and the lack of research on BMAA production, this toxin is not covered further in this report.

### **Cylindrospermopsins**

Cylindrospermopsin is a tricyclic alkaloid (Figure 3D) that is a potent protein synthesis inhibitor and causes extensive damage to the liver and kidney (Terao et al. 1994; Falconer et al. 1999). There is evidence that cylindrospermopsin may also act as a tumour initiator (Falconer & Humpage 2001). Multiple cylindrospermopsin analogues exist (Norris et al. 1999; Banker et al. 2000) and they have been reported from a range of cyanobacteria and geographic locations, including Aotearoa New Zealand (Wood & Stirling 2003). In 1979, cylindrospermopsin was implicated in a significant human poisoning case when 148 people were hospitalised with symptoms of gastroenteritis after a water supply on Palm Island (Australia) was dosed with copper sulphate to control a dense *Raphidiopsis raciborskii* bloom. The copper sulphate lysed the cells and released cylindrospermopsins into the drinking water supply (Byth 1980; Bourke et al. 1983; Hawkins et al. 1985).

### **Microcystins and nodularins**

Globally, microcystins are the most frequently reported cyanotoxin (Harke et al. 2016; Chorus & Welker 2021). Microcystins are heptapeptides containing five D- and two L-amino acids, including the unique  $\beta$ -amino acid Adda (Figure 3E). To-date, more than 250 microcystin variants have been isolated and characterised (Chorus & Welker 2021), providing challenges for their identification and measurement in environmental samples. Nodularins are structurally related to microcystins and contain Adda, but nodularins are pentapeptides containing only five amino acids (Figure 3F).

Each microcystin variant differs with respect to the methyl groups and two L-amino acids within the cyclic peptide ring. This results in pronounced differences in the toxicity of variants. Less structural variability has been observed with nodularins, which may be due to a range of reasons including less research being conducted on the toxin class compared to microcystins. Microcystins and nodularins are hepatotoxins that inhibit protein phosphatases 1 and 2A in affected organisms (MacKintosh et al. 1990; Honkanen et al. 1991). Numerous incidents of animal and

human poisonings have been attributed to microcystins and nodularins (Ressom et al. 1994). One of the most severe cases occurred in Brazil in 1996, when the water supply to a hospital was contaminated with microcystins resulting in dialysis water containing ~20 µg/L. This resulted in 56 fatalities at a dialysis treatment clinic in the hospital (Azevedo et al. 2002).

Whilst a broad range of cyanobacterial genera produce microcystins, most reports of nodularin are associated with *Nodularia spumigena*, which primarily grows in brackish water (Chorus & Welker 2021). However, nodularin has also been observed in *Iningainema pulvinus* from an Australian wetland (McGregor & Sendall 2017) and a *Nostoc* species that grows symbiotically with cycads (Gehring et al. 2012). Nodularin has also been detected in cyanobacteria mats from Lake Tikitapu (Wood et al. 2012b) and rivers in California (USA; Gehring et al. 2012; Kelly et al. 2019). Whilst the nodularin producer was not identified in Lake Tikitapu, a *Nodularia* sp. cohabiting in the algal mats (as a minor taxa) was responsible for the nodularin observed in the samples from Californian rivers (Kelly et al. 2019).

### Saxitoxins

Saxitoxins are alkaloids (Figure 3G) that inhibit nerve conduction by blocking sodium channels (Adelman et al. 1982). They are commonly produced by marine dinoflagellates under the name of paralytic shellfish toxins. Whilst saxitoxins from freshwater cyanobacteria have not been associated with human deaths, they have killed animals (Negri et al. 1995). They were identified in an extensive bloom of *Dolichospermum circinale* on the Murray Darling River (Australia), which resulted in the death of over 1,600 sheep and cattle (Bowling & Baker 1996).

### Lipopolysaccharides

Lipopolysaccharides (LPS) are integral components of the cell wall for all gram-negative bacteria, including cyanobacteria. LPS is found in the outer cell membrane and forms complexes with proteins and phospholipids (Chorus & Welker 2021). Exposure to LPS can elicit irritant and allergenic effects in humans and animals (Torokne et al. 2001; Pilotto et al. 2004) including from exposure to cyanobacteria (Ressom et al. 1994). Because of the limited information on these toxins in cyanobacteria, they are not covered further in this report.

#### 2.4.2. Accumulation of cyanotoxins in aquatic foodstuffs

As with other toxins, cyanotoxins can accumulate in food webs leading to the contamination of foodstuffs consumed by humans. Below is a brief summary of global knowledge on the accumulation of cyanotoxins in aquatic foodstuffs and information on studies conducted on foodstuffs native to Aotearoa New Zealand.

### Fish

International research has shown that microcystins can accumulate in both freshwater and marine fish (Magalhães et al. 2003; Mohamed et al. 2003). Generally, the highest

toxin levels were found in the liver, but toxin was also detected in the muscle tissue. Microcystin accumulation has been studied in rainbow trout from the Te Arawa lakes in the Rotorua region. A study where trout were exposed to microcystin-contaminated lake water showed that microcystins accumulated in both the liver and flesh of rainbow trout (Wood et al. 2006a). To the best of our knowledge, no work has been done on microcystin accumulation in marine fish species in Aotearoa New Zealand.

International research has shown that cylindrospermopsin accumulates in some fish species but not in others (Kinnear 2010). To the best of our knowledge, no studies have evaluated cylindrospermopsin accumulation in fish species from Aotearoa New Zealand.

### **Tuna / eels**

A study on tuna / eels from Wairewa / Lake Forsyth (Canterbury region) showed that nodularin accumulated in the liver and flesh (Dolamore et al. 2017). Higher nodularin concentrations were observed in the liver compared to the flesh. Similar observations have also been made in tuna from Whakakī Lake in Hawke's Bay (personal knowledge from Jonathan Puddick). An international study showed that microcystins can accumulate in silver eel livers following natural exposure to the toxin (Acou et al. 2008); however, flesh samples were not assessed during this study.

### **Shellfish**

Microcystin can accumulate in freshwater mussels and clams (Eriksson et al. 1989; Prepas et al. 1997). Research from Aotearoa New Zealand has shown that microcystin can accumulate in kākahi (freshwater mussels) in both a natural lake setting (Wood et al. 2006a) and during feeding studies (Clearwater et al. 2014).

International research has shown that microcystins (contained within cyanobacteria) are taken up by shellfish and are accumulated primarily in the gut but also to a lesser degree in the flesh (Chen et al. 1993; Vasconcelos 1995; Williams et al. 1997; Amorim & Vasconcelos 1999). This research has shown that microcystin was depurated in a similar manner to that observed with marine algal toxins and that after a depuration period, microcystin was cleared from the shellfish (Vasconcelos 1995; Williams et al. 1997; Amorim & Vasconcelos 1999). The deaths of 21 southern sea otters in Monterey Bay (California, USA) during 2007 was linked to microcystin-producing *Microcystis* flowing out of lake systems and accumulating in marine shellfish (Miller et al. 2010). This demonstrates the potential health risk posed by freshwater cyanotoxins entering a marine environment used for food harvesting.

There is very little information on the accumulation and depuration of microcystins in marine shellfish found in Aotearoa New Zealand. Microcystin was detected in Pacific oysters from Hokianga Harbour in 2005 (Holland et al. 2005). The detection was made using an Adda-ELISA test, which can be subject to cross-reactivity and can sometimes yield false positives. A follow-up study showed that microcystins were not

detected by liquid chromatography-mass spectrometry (LC-MS) in Pacific oysters fed with microcystin-producing *Microcystis* (Wall et al. 2014).

Saxitoxin accumulation, from marine microalgae, in marine shellfish is well documented internationally (Etheridge 2010) and in Aotearoa New Zealand (MacKenzie 2014). For this reason, saxitoxins are commonly referred to as paralytic shellfish toxins. The accumulation, depuration and physiological effects of saxitoxins on native shellfish species in this country has been investigated in green-lipped mussels, Bluff oysters, flat oysters, New Zealand scallops and clams (ringed venus shell and southern tuatua; Marsden & Shumway 1992; Contreras et al. 2011, 2012; Harwood et al. 2013).

The accumulation of saxitoxin, produced by freshwater cyanobacteria, has also been recorded in international studies on freshwater and marine mussels (Negri & Jones 1995; Pereira et al. 2004; Ramos et al. 2021). *Cuspidothrix issatschenkoi* (previously *Aphanizomenon issatschenkoi*), *Dolichospermum circinale* (previously *Anabaena circinalis*) and *R. raciborskii* were the saxitoxin-producing cyanobacteria in these studies.

Cylindrospermopsin accumulation has been studied in freshwater mussels (swan mussel, *Anodonta cygnea*) with the highest concentrations being present in the haemolymph (Saker et al. 2004).

### **Crustaceans**

Accumulation of nodularin in Aotearoa New Zealand's endemic freshwater crayfish (kōura) has been demonstrated in a natural lake setting (Wood et al. 2012c). An experimental feeding study using kōura also demonstrated uptake of microcystins (Clearwater et al. 2014). Microcystin accumulation was most pronounced in the hepatopancreas, but the toxin was also detected in the flesh.

International research has shown that microcystin accumulates in marine crustaceans (Vasconcelos et al. 2001; Magalhães et al. 2003; Garcia et al. 2010). Whilst toxin levels were generally most evident in the hepatopancreas, microcystin was also observed in the flesh. To the best of our knowledge, no studies have been conducted on the accumulation of freshwater cyanotoxins in marine crustaceans from Aotearoa New Zealand.

Cylindrospermopsin has been shown to accumulate in redclaw crayfish (Saker & Eaglesham 1999). Cylindrospermopsin was detected in both the flesh and the hepatopancreas, but higher levels were observed in the hepatopancreas.

### **Anatoxin accumulation in aquatic foodstuffs**

Little work has been performed on the accumulation of anatoxins in aquatic food webs and foodstuffs. There has been one report from France of a food poisoning event

related to consumption of sea figs (tunicates of the genus *Microcosmus*) contaminated with anatoxin-a (Biré et al. 2020). After eating sea figs, 26 patients suffered from blurred or double vision, ataxia and dizziness, asthenia, headache, muscle cramps, paresthesia and digestive disorders (nausea, vomiting and diarrhoea). Anatoxin-a was detected in food remains, up to concentrations of 1,240 µg/kg.

Anatoxins produced by *Microcoleus* (dihydroanatoxin-a) have also been experimentally shown to accumulate in the tissues of aquatic macroinvertebrates (Kelly et al. 2020); however, the concentration of dissolved toxin used in the study is unlikely to be observed in the natural environment. There is a lack of data on whether anatoxins biomagnify into higher trophic levels (e.g., tuna / eels, trout, salmon) and potentially pose a risk to people.

### **2.4.3. Effects of cyanobacteria on ecosystems and food webs**

#### **Lake ecosystems**

Because phytoplankton form a basal part of food webs, small to moderate shifts in their community can result in changes to higher trophic levels of the lake ecosystem (e.g., invertebrates, bivalves, crustaceans, fish; Sukenik et al. 2015). For example, because larger zooplankton do not preferentially feed on cyanobacteria, the zooplankton community tends to be dominated by smaller types (Heathcote et al. 2016; Ersoy et al. 2017). Smaller zooplankton provide a less efficient food source for fish (that feed on zooplankton), as they need to invest more time searching for and consuming them. This effect is also compounded by poor visibility from the turbidity created by cyanobacteria in the water, reducing the fishes' search efficiency (Ersoy et al. 2017). Ultimately this affects the abundance, size and health of fish in the ecosystem. Changes in lake food webs are particularly relevant in Aotearoa New Zealand, where Māori culture highly values the consumption of mahinga kai (gathered food) and rural Māori communities rely on it as a staple foodstuff (Guy et al. 2021).

Larger shifts in the phytoplankton community towards dominance by cyanobacteria (i.e., blooms), will cause more dramatic effects to lake ecosystems. Cyanobacteria blooms in lakes can cause large diurnal fluctuations in dissolved oxygen levels due to cyanobacteria photosynthesising during the day (producing oxygen) and respiring at night (consuming oxygen). When the bloom dies off, heterotrophic microbes feed on the decaying cyanobacteria, also depleting oxygen in the water (Havens 2008; Sukenik et al. 2015). This dissolved oxygen depletion in the lake water can cause fish and invertebrates to suffocate, and sometimes results in mass die-offs. Dense populations of cyanobacteria on the surface of lakes (e.g., scums) can also smother aquatic plants by decreasing light penetration and limiting gas exchange (Havens 2008; Sukenik et al. 2015). As described above, this will impact higher trophic levels of the lake ecosystem as aquatic plants form a basal part of lake food webs.

### River and stream ecosystems

Shifts in the composition of the periphyton community toward cyanobacterial dominance can have an impact on the ecology of rivers and streams. As with lakes, high cyanobacterial biomass is associated with extreme diurnal dissolved oxygen shifts. Anoxia events (depletion of oxygen that suffocates fish and invertebrates) are uncommon in rivers and streams due to turbulent flow and atmospheric oxygen diffusion, but localised anoxia can occur under dense accumulations of decomposing cyanobacterial mats.

*Microcoleus* proliferations have been associated with changes in the macroinvertebrate community in rivers and streams (Wood et al. 2014b). Whilst anatoxins purified from environmental *Microcoleus*-dominated mats had no acute effects on *Deleatidium* spp. (mayfly) larvae (Kelly et al. 2020), acute exposure to crude *Phormidium* extracts (also containing anatoxin-a) resulted in significant mortality in three macroinvertebrate taxa; *Chironomus dilutus*, *Ceriodaphnia dubia* and *Hyaella azteca* (Anderson et al. 2018). This suggests that anatoxins are not the cause of macroinvertebrate shifts relating to *Microcoleus* proliferations and that other compounds are likely the cause.

#### 2.4.4. Downstream problems in rivers, streams and estuaries

##### Downstream issues from planktonic cyanobacteria

Although planktonic freshwater cyanobacteria primarily exist in lake ecosystems, elevated levels of planktonic cyanobacteria in lakes also lead to downstream problems in rivers, streams, and estuaries. This occurs both here in Aotearoa New Zealand (Wood et al. 2005; Kouzminov et al. 2007; Wall et al. 2014) and in other countries (Miller et al. 2010; Bowling et al. 2013; Gobble & Kudela 2014; Lance et al. 2021). In slow-flowing rivers and streams, the cyanobacteria may function as if they are in a lake ecosystem and continue to grow, but once they reach marine environments, increased salt concentrations will cause the cells to eventually die off. Increased frequency, duration and intensity of cyanobacterial blooms in lakes, and higher levels of toxin-producing taxa, will also result in human health risks in the outflowing rivers of lakes suffering from cyanobacterial blooms, and in the estuaries they flow into.

When toxin-producing cyanobacteria flow into estuarine systems where shellfish grow, the accumulation of cyanotoxins in the shellfish is well documented internationally but less so in Aotearoa New Zealand (see Section 2.4.2). With sufficient time, the toxins are eventually depurated from the shellfish. For example, Pereira et al. (2004) found that saxitoxins produced by cyanobacteria depurated from shellfish to below the limit of detection after 14 days. Toxin accumulation and depuration rates vary between shellfish types and the lack of Aotearoa New Zealand studies in this area makes it difficult to advise on the risk.

**Downstream issues from benthic cyanobacteria**

Downstream problems resulting from benthic cyanobacterial proliferations are twofold. Firstly, detaching benthic mats can wash up on shorelines downstream, presenting a health hazard even when a downstream site has little obvious signs of benthic cyanobacteria. This risk is currently mitigated by assigning a higher risk category to recreational bathing sites with signs of cyanobacterial mats washed ashore (MfE & MoH 2009). Higher water temperatures and larger biomass accumulation of benthic cyanobacteria increases the risk of the mats detaching from the substrate and washing downstream, which poses the greatest hazard at unmonitored sites with low- or no-visible cyanobacterial coverage within the river or stream itself. Secondly, the toxins produced by benthic cyanobacteria are known to travel downstream and can contaminate food sources at long distances from the initial cyanobacterial biomass (Miller et al. 2010). Although the release of anatoxins has been demonstrated in Aotearoa New Zealand (Wood et al. 2018), there is less evidence of toxin release by other benthic cyanobacteria and the associated hazard from toxins produced by benthic cyanobacteria is unclear.

### 3. CLIMATE CHANGE IN LAKES, RIVERS AND STREAMS AND IMPACTS ON PROBLEMATIC CYANOBACTERIA

In this section we review international research that has explored the impact of climate change on cyanobacteria. We begin with a brief overview of the predicted impacts of climate change on lakes and rivers globally and refer readers to reviews and studies that cover this topic in greater detail.

We then provide a detailed commentary of the specific factors that are predicted to directly impact planktonic and benthic cyanobacteria (e.g., temperature, river and stream flows). The impact of these variables on toxin production is covered in Section 4. More specific information on projected climate change impacts on cyanobacteria in lakes, rivers and streams in Aotearoa New Zealand is provided in Section 5.

#### 3.1. Overview of the impact of climate change on lakes, rivers and streams

##### 3.1.1. Lakes

The measured and predicted impacts of climate change on lake ecosystems globally and regionally have been reviewed in detail by numerous authors (e.g., Mooij et al. 2005; Dokulil et al. 2010; Woolway et al. 2020). The specific effects are likely to vary geographically and with lake type, but the most commonly reported and predicted impacts include:

- increases in lake surface water temperature that will have flow-on effects, including prolonged summer stratification, increased oxygen depletion and changes in the distribution of cold or warm intolerant species. Growth rates of organisms at all tropical levels such as fish, algae and zooplankton are likely to increase, but not at the same rate for each species, which will impact food web dynamics. Rates of metabolism will also increase across trophic levels.
- decreases in winter ice cover, which will impact nutrient cycling, mixing regimes and likely cause shifts in species composition
- increased evaporation rates
- changes in residence times, impacting nutrient cycling
- more severe storm events, interspersed with longer periods of stable, high temperatures will impact lake mixing and increase the input of dissolved nutrients and other contaminants and increase the release of sediment-bound nutrients
- increased dissolved CO<sub>2</sub> concentrations in lake water will lower the pH, potentially impacting productivity and sensitive organisms
- increased salinity in coastal lakes, due to sea-level rise.

### **3.1.2. Rivers and streams**

The impact of climate change on rivers and streams will vary regionally and be dependent on the location and size of the river and streams. The alteration in both temperature and precipitation are the most important physical effects of climate change on river ecosystems and is recently reviewed in Siddha and Sahu (2022) and Gudmundsson et al. (2021). Projected changes in storm frequency, precipitation intensity, groundwater runoff, snowfall and the timing of snow melt will all impact river flows (MfE & Stats NZ 2020). Increased temperatures will change dissolved oxygen dynamics, as well the growth and metabolic rates of species (St-Hilaire et al. 2021; Rajesh & Rehana 2022). These changes will not be uniform across all species and there will be changes in species composition due to temperature intolerances of some taxa (MfE & Stats NZ 2020). As noted for lakes, increased dissolved CO<sub>2</sub> will also lower river water pH, potentially impacting sensitive organisms.

## **3.2. Planktonic cyanobacteria**

As described above the key variables that will shift under climate change are increased temperatures, changes in mixing regimes and associated nutrient cycling, changes in food webs, shifts in dissolved CO<sub>2</sub> and pH, and increases in salinity for coastal lakes. Each of these changes will impact the growth and ecology of planktonic cyanobacteria, and likely outcomes and key studies on these topics are summarised below.

### **3.2.1. Increased temperatures**

At temperatures above 25 °C, cyanobacteria growth rates generally continue to increase whereas growth rates for eukaryotic phytoplankton (e.g., diatoms and green algae) stabilise or decrease (Canale & Vogel 1974; Peperzak 2003; Reynolds et al. 2006; Jöhnk et al. 2008). Increased lake water temperatures will likely provide a competitive advantage to cyanobacteria, resulting in a shift in the phytoplankton community to a state where cyanobacteria are more prevalent and abundant.

Beyond differences in growth rates, higher water temperatures also result in physical changes to surface waters that provide additional advantages for cyanobacteria. Water viscosity decreases at higher temperatures, aiding nutrient diffusion towards the cell surface for absorption. Because certain cyanobacterial species have strategies for nutrient scavenging and storage (Mur et al. 1999), they are well positioned to out-compete other phytoplankton by making use of increased access to nutrients. Reduced water viscosity also promotes the sinking of heavier non-motile phytoplankton (e.g., diatoms) limiting their access to the light available in the surface waters of a lake. Because many cyanobacteria are able to control their buoyancy (Mur et al. 1999), they are not similarly affected and can dominate in high-light and low-viscosity surface waters.

### ***3.2.2. Stratification and associated nutrient release***

During sustained warm periods, 'stratification' of lakes can occur. When a lake stratifies, the warmer surface waters (epilimnion), and the cooler bottom waters (hypolimnion) do not mix. Because oxygen exchange does not occur between the epilimnion and hypolimnion when the lake is stratified, oxygen levels in the bottom waters decline until they become anoxic. At this point, anaerobic bacteria in the lake sediments become more active and this results in the liberation of nutrients from lake sediments (due to anaerobic metabolic pathways the microbes use to grow). While the lake remains stratified, the liberated nutrients remain in the bottom waters of the lake. But when the lake remixes, the nutrients become freely available to support phytoplankton growth in the lake.

The longer periods of higher temperatures (heat waves) predicted with continued climate change will lead to increased frequency, strength and duration of lake stratification. This will result in an increase in the levels of nutrients released in anoxic bottom waters, exacerbating lake eutrophication and the subsequent shifts in lake ecosystems. As certain cyanobacteria can regulate their buoyancy, periods of lake stratification give them a competitive advantage over phytoplankton that cannot. Buoyancy allows cyanobacteria to migrate between light-rich surface waters (where they can photosynthesise to produce energy stores) and nutrient-rich bottom waters (allowing sustained growth and reproduction). Longer periods of lake stratification will result in cyanobacteria being able to dominate the lake ecosystem for larger portions of the year and the nutrients released will fuel cyanobacterial abundance upon remixing.

### ***3.2.3. Increased storm and drought intensity and frequency***

In some regions of the globe, storm and drought events will increase in frequency and intensity. Storm events can result in rapid nutrient enrichment of lakes, which has been shown to cause the early onset of cyanobacterial blooms (Reichwaldt & Ghadouani 2012; Larsen et al. 2020). Droughts can change residence time, alter mixing regimes, lead to warmer water temperatures and increase nutrient concentrations—all conditions that favour the proliferation of cyanobacteria. In a study of 40 artificial lakes, Brasil et al. (2016) found evidence that warmer and drier climates reduce water quantity and increase cyanobacterial blooms.

### ***3.2.4. Changes in food webs***

As discussed above, temperature and nutrient changes will directly impact cyanobacteria. These changes will also have indirect impacts on the growth rates and metabolism of organisms that feed on cyanobacteria, most notably zooplankton (Ger et al. 2014). There could also be flow-on effects higher in the food web with changes in fish composition, etc. While several studies have explored the impact of climate change on zooplankton (Vadadi-Fülöp et al. 2012; Carter et al. 2017), to the best of

our knowledge, robust experiments have not explored how climate change will impact interactions between lake food webs, and therefore the effect on cyanobacteria.

### 3.2.5. Increased dissolved CO<sub>2</sub> and reduced water pH

There is a large body of data on growth rates of marine cyanobacteria under changing dissolved CO<sub>2</sub> concentrations, but there are limited studies on freshwater cyanobacteria. From the studies on marine cyanobacteria, some observed lower growth rates for certain cyanobacteria species with increased dissolved CO<sub>2</sub> (Shapiro 1990; Whitton & Potts 2000; Czerny et al. 2009) whilst other studies observed increased growth rates (Hein & Sand-Jensen 1997; Fu et al. 2007; Levitan et al. 2007; Kranz et al. 2009).

Although *Microcystis* blooms are rarely thought to be carbon-limited due to the ability for *Microcystis* to use both CO<sub>2</sub> and bicarbonate uptake pathways, Verspagen et al. (2014) found higher growth rates and biomass at higher CO<sub>2</sub> levels using chemostat culturing experiments. With low CO<sub>2</sub> and saturated bicarbonate conditions, the culture was unable to sustain high biomass (Verspagen et al. 2014). These observations suggest that higher dissolved CO<sub>2</sub> concentrations will promote *Microcystis* growth. Rising atmospheric CO<sub>2</sub> levels may also influence the composition of toxic and non-toxic genotypes. In chemostat experiments using mixed cultures of toxic and non-toxic *M. aeruginosa*, non-toxic *M. aeruginosa* became dominant at high-CO<sub>2</sub> levels but only under low light conditions (van de Waal et al. 2011). The toxic *M. aeruginosa* strain grew best at low-CO<sub>2</sub> concentrations. In contrast, the growth and nitrogen fixation rates of *N. spumigena* was reduced with elevated dissolved CO<sub>2</sub> concentrations (Czerny et al. 2009). These observations suggest that increasing dissolved CO<sub>2</sub> concentrations may influence the composition of phytoplankton and cyanobacterial communities in lakes.

### 3.2.6. Salinity

Climate-induced rises in sea level are likely to result in increased saltwater inductions into many coastal lakes. There is considerable uncertainty on how this will impact cyanobacteria. Coastal lakes are often at the bottom of catchments and highly eutrophic. While some freshwater cyanobacteria such as *Microcystis* can cope with a degree of salinity (Melero-Jiménez et al. 2020), most cannot. A likely scenario is that there will be a compositional shift in these lakes, towards dominance of brackish water species such as *N. spumigena*.

## 3.3. Benthic cyanobacteria

As described in Section 3.1 above, the key variables that will shift in rivers under climate change are increased temperatures, changes in river and stream flows and

associated nutrient and sediment inputs, and pH. The potential impact of these changes on benthic cyanobacteria are discussed below.

### **3.3.1. Increased temperatures influencing growth rates and community composition**

Increased water temperatures are likely to cause a rise in the prevalence and severity of benthic cyanobacterial proliferations. Cyanobacteria have higher temperature optima for growth than many other periphyton classes such as dinoflagellates, diatoms and green algae (Paerl et al. 2011; Burford et al. 2020; Griffith & Gobler 2020) enabling them to outcompete other taxa. Temperatures above 15 °C resulted in the dominance of cyanobacteria over diatoms in laboratory experiments (Watermann et al. 1999). A recent analysis of a 20-year dataset of benthic algae in two pristine Norwegian streams also forecast greater *Phormidium* cover with increasing temperatures (Schneider 2015). Heath et al. (2011) demonstrated that water temperature and river flow were the two main factors driving the presence of *Microcoleus* mats. A follow-up study demonstrated that river water temperatures above 14 °C favoured the development of *Microcoleus* proliferations in New Zealand rivers (Heath et al. 2015).

Warmer temperatures can also modify cyanobacterial physiology in synergy with other environmental variables, giving them additional advantages over other periphyton classes. For example, nitrogen-fixing, benthic cyanobacterial genera such as *Nostoc* and *Anabaena* increase their nitrogen-fixation rates as temperatures increase (Reuter et al. 1983; Scott & Marcarelli 2012). Marcarelli & Wurtsbaugh (2006) found a two-fold increase in nitrogen-fixation rates with an increase in temperature from 13–18 °C. Increased capacity for nitrogen-fixation reduces the reliance of these cyanobacteria on external nitrate sources, allowing them to outcompete other periphyton at lower nitrate concentrations.

A recent study that used multivariate analyses to characterise the most important factors regulating a variety of benthic cyanobacteria in the northeastern USA found that each genus examined exhibited different responses, but also found that increasing temperature was an important factor in the growth of many species (Schulte et al. 2022).

### **3.3.2. Shifts in rainfall patterns**

Climate change is predicted to cause shifts in rainfall through a) strengthening of existing patterns, i.e., wet regions become wetter and dry regions become drier; and b) changing storm tracks, which should move away from the equator and toward the poles as atmospheric circulation changes (Trenberth 2011).

As mentioned in Section 3.3.1 above, Heath et al. (2011) demonstrated that water temperature and flow were the two main factors driving the presence of *Microcoleus* mats in rivers. The researchers observed a marked increase in mats when river flows

decreased below one-half of the yearly average and at water temperature over 14 °C. Using an in-stream habitat assessment method, Heath et al. (2015) showed that decreases in summer minimum low flows resulted in negligible change to available *Microcoleus* habitat (Heath et al. 2015). The authors concluded that the frequency of flushing flows (a flow that removes the *Microcoleus* from the river substrate), and not flow itself, was critical in determining the presence of *Microcoleus*.

The recolonisation and community composition of biofilms in rivers following a flushing-flow event exhibits distinct successional stages (Brasell et al. 2015). Intermittent and extreme disturbance events resulting from significant rainfall can alter the composition of the benthic community (Lukács et al. 2021), which may result in more resistant taxa dominating the community following repeated high-flow events. These results are from short-term studies that focus on specific flow events, rather than monitoring disturbances over long periods of time. There are few monitoring datasets that include regular assessments of benthic cyanobacterial growth in combination with rainfall and river flow data.

### 3.3.3. Benthic cyanobacteria in lakes

There is little research on benthic cyanobacteria in lakes and their potential responses to drivers that will change with climate change (e.g., increased temperatures). Benthic cyanobacteria are common in alpine tarns, where the clear, shallow water and high stability are favourable for growth. Like their river-inhabiting counterparts, lake-dwelling benthic cyanobacteria are likely to benefit from increasing water temperatures. One benthic-lake cyanobacterial species, *Microseira wollei* (formerly *Lyngbya wollei*) exhibits the highest growth rate at 26 °C, with lower growth rates below 10 °C (Yin et al. 1997). It is likely that benthic cyanobacteria in lakes will respond to increased water temperatures in a similar manner to other planktonic and benthic cyanobacteria, with increased growth rates if they do not experience light limitation from shading by planktonic cyanobacteria.

There is also the potential for salt-tolerant benthic cyanobacteria species such as *Lyngbya* and *Oscillatoria* to become more prevalent in littoral zones of lakes affected by increased salinity due to sea level rise (Paerl & Fulton 2006).

## 4. CLIMATE CHANGE AND TOXIN PRODUCTION

Environmental variables regulating cyanotoxin production have been a topic of intense interest over recent decades; however, the research is highly biased towards understanding the triggers for microcystin production. Most studies use laboratory cultures and only demonstrate modest changes in toxin production (3- to 4-fold). Recent field studies on microcystin production have indicated that larger shifts in toxin production (18- to 362-fold) are possible in natural communities (Wood et al. 2011; Wood et al. 2012a; Puddick et al. 2016; Wood et al. 2021). This section reviews research on toxin regulation related to variables that are expected to shift with climate change: temperature, dissolved carbon dioxide concentration and cell density (as a result of increased severity of cyanobacterial blooms). This content has been adapted from Wood et al. (2015b) and Kelly et al. (2021).

### 4.1. Anatoxins

Rapala et al. (1993) studied anatoxin production in *Dolichospermum* (described as *Anabaena* in the study) and *Aphanizomenon* and demonstrated that high temperature decreased the amount of the toxin produced regardless of growth rates. Rapala & Sivonen (1998) evaluated anatoxin production in *Dolichospermum* strains and observed slightly higher anatoxin-a production at temperatures lower than the growth optimum. Shifts in the relative production rates of anatoxin variants were observed at different temperatures and with different carbon sources in benthic *Oscillatoria* sp. (Aráoz et al. 2005). Anatoxin-a production was increased at 22 °C when the growth medium was not enriched with CO<sub>2</sub>, whilst homoanatoxin-a production was higher at 25 °C and supplementation with bicarbonate.

Field and laboratory studies have demonstrated that *Microcoleus* mats are commonly a mixture of toxic and non-toxic genotypes. Among toxic genotypes, anatoxin concentrations can vary up to 100-fold (Wood et al. 2010b; Wood et al. 2012d). Heath et al. (2011) undertook a one-year study at eight sites on two rivers and observed that anatoxin-a and homoanatoxin-a occurrence was restricted to where water temperature exceeded 13.4 °C (Heath et al. 2011), and suggested that the toxin-producing strains may 'out-compete' non-toxic *Microcoleus* strains under these conditions. Other research has shown no correlation between water temperature and toxin production (Wood et al. 2012d; Wood & Puddick 2017) or the relative abundance of toxic strains (Kelly et al. 2018). In contrast, the toxin content of proliferations of the benthic anatoxin-producing genus *Tychonema* was positively correlated with higher temperatures (Bauer et al. 2022), although this association requires further investigation.

## 4.2. Cylindrospermopsins

Saker and Griffiths (2000) explored the effect of temperature (20–35 °C) on growth and cylindrospermopsin content in *R. raciborskii* and found a strong negative correlation between toxin content and temperature. Cylindrospermopsin was not detected in the strains grown at 35 °C. However, when the cultures were transferred back to lower temperatures, cylindrospermopsin production was restored. Mohamed Nor et al. (2019) evaluated cylindrospermopsin production in *R. raciborskii* at four temperatures between 25–38 °C and cylindrospermopsin quotas were highest at 25 °C. A study has investigated the effect of elevated dissolved CO<sub>2</sub> levels on cylindrospermopsin production and release in *R. raciborskii* (Pierangelini et al. 2015). At higher dissolved CO<sub>2</sub> levels, slightly higher cylindrospermopsin quotas were measured and this was coupled with higher levels of extracellular cylindrospermopsin. Because no significant change in cylindrospermopsin synthase gene expression was observed, the researchers felt the observed changes in cylindrospermopsin were more likely due to natural variability rather than an up-regulation in production.

Preußel et al. (2009) highlighted how toxin production can vary among strains of the same species. They investigated the influence of light and temperature on cylindrospermopsin production in two *Aphanizomenon flos-aquae* strains at three temperatures between 16 and 25 °C. Cylindrospermopsin concentrations significantly decreased with increasing temperature in one strain, but the other strain demonstrated no clear relationship between toxin production and temperature.

## 4.3. Microcystins

Many early studies focused on the effect of temperature on microcystin production and showed that toxin concentrations were maximal between 20 to 25 °C and decreased at higher and lower temperatures (van der Westhuizen & Eloff 1985; Watanabe & Oishi 1985; Codd & Poon 1988; Sivonen 1990; Rapala & Sivonen 1998; Amé & Wunderlin 2005; Dziallas & Grossart 2011; Bui et al. 2018). In contrast, a study undertaken using tropical *Microcystis* species from Singapore indicated that maximal microcystin production was at higher temperatures (30–33 °C) for most of the strains evaluated (Mowe et al. 2015). As with the studies mentioned earlier, decreased microcystin production was observed at higher temperatures (36 °C in this instance; Mowe et al. 2015). These observations between temperate and tropical strains suggest that the ambient temperature cyanobacteria have evolved to live in plays a role in how toxin production changes with temperature.

Geada et al. (2017) found that microcystin production was approx. 2,000-fold lower under high-temperature, high-CO<sub>2</sub> and high-light (30 °C, 7.5% v/v CO<sub>2</sub> and 155 μmol photons/m<sup>2</sup>/s). Because multiple environmental parameters will be simultaneously affected by climate change (e.g., temperature and dissolved CO<sub>2</sub> concentrations),

experiments evaluating the effects of interacting parameters are particularly valuable for understanding the impacts of climate change.

Changing temperatures may also influence the levels of different microcystin congeners and the toxicity of cyanobacterial strains (due to the differing potencies of microcystin congeners). At 20 °C, cultures and natural populations of *Microcystis aeruginosa* would switch from predominantly microcystin-LR to predominantly microcystin-RR (a less toxic phenotype). At 28 °C, microcystin-LR and microcystin-RR production remained constant (Amé & Wunderlin 2005). A similar observation was made in *Microcystis viridis* where higher proportions of microcystin-RR were observed at lower temperatures (15–20 °C; Song et al. 1998).

The effects of pH and dissolved CO<sub>2</sub> on microcystin production has not been well studied. It has been suggested that *Microcystis* is more toxic at high and low pH values corresponding to slower rates of growth (van der Westhuizen & Eloff 1983). Jähnichen et al. (2007) studied the impact of inorganic carbon availability on microcystin production, and suggested that microcystins may be involved in enhancing the efficiency of the adaptation of the photosynthetic apparatus to fluctuating inorganic carbon concentrations. van de Waal et al. (2009) showed that an excess supply of both nitrogen and carbon resulted in high cellular nitrogen:carbon (N:C) ratios along with microcystin quotas and the nitrogen-rich variant microcystin-RR (van de Waal et al. 2009). Comparable patterns were found in lakes dominated by *Microcystis*, where the relative microcystin-RR content increased with the N:C ratio.

Using field-based studies, Wood et al. (2011) showed that *Microcystis* sp. can ‘switch’ microcystin production on and off, with the trigger relating to increased cell density and ‘scum’ formation. When a surface scum of *Microcystis* sp. formed on the lake edge (a dense accumulation of buoyant cells forced together by light winds), microcystin quotas increased by 28-fold over a five-hour period and coincided with a 462-fold increase in microcystin-synthetase subunit-E (*mcyE*) gene expression (Wood et al. 2011). In a follow-up study the researchers also experimentally induced an 18-fold increase in microcystin quotas within a six-hour period by increasing the *Microcystis* cell density in mesocosms (Wood et al. 2012a). Further work on field samples collected from a lake experiencing a *Microcystis* bloom yielded similar observations, that increased *Microcystis* cell densities lead to increased microcystin quotas (up to 362-fold differences in microcystin quota were observed; Wood et al. 2021). Puddick et al. (2016) saw similar increases in microcystin quotas when testing fine-scale cryogenic samplers. The new sampling technique allowed the researchers to demonstrate that the increased microcystin production was only occurring in the top 5-mm of the water column. All of these studies and a recent laboratory study (Pereira & Giani 2014) draw a correlation between microcystin production and cyanobacteria cell densities. This suggests that toxin production per cell may increase if *Microcystis*

blooms and scum formations intensify as is predicted under future climate change scenarios (Paerl & Huisman 2008).

#### 4.4. Nodularins

Little work has been performed on the environmental parameters that affect nodularin production. Early studies indicated that nodularin production in *N. spumigena* was generally highest under conditions that promoted growth; e.g., higher temperatures, irradiance and phosphate concentrations (Lehtimäki et al. 1994; Lehtimäki et al. 1997). Silveira & Odebrecht (2019) made similar observations in *N. spumigena* from Brazil, that nodularin production was most closely linked to factors that encouraged growth, including temperature. Higher nodularin quotas were generally observed in cultures grown at 30 °C compared to those grown at 23 °C and 15 °C.

Mazur-Marzec et al. (2005) demonstrated a very clear positive effect of salinity on nodularin production in *N. spumigena*. Silveira & Odebrecht (2019) also evaluated how salinity influenced nodularin production in *N. spumigena*, but results were inconsistent and no trends were evident.

#### 4.5. Saxitoxins

Studies on the effects of temperature have been undertaken in two saxitoxin-producing cyanobacterial taxa; *Aphanizomenon* sp. and *R. raciborskii*. In *Aphanizomenon* sp., Dias et al. (2002) observed increased saxitoxin production at a higher growth temperature (28 °C versus 22 °C). A study evaluating saxitoxin production and transport in *Aphanizomenon gracile* grown at a range of temperatures found that both production and extracellular transport were greatest at the highest temperature assessed (30 °C; Cirés et al. 2017). In *R. raciborskii*, Castro et al. (2004) found that there was no significant change in toxin concentration when grown at 19 and 25 °C. However, at 25 °C the saxitoxin congener profile shifted and an additional saxitoxin variant (dcSTX) was detected. Another study investigating saxitoxin production in three strains of *R. raciborskii* at four temperatures between 15 and 30 °C observed the highest levels of saxitoxin production at 25 °C, with a large drop in saxitoxin production at 30 °C (Mesquita et al. 2019). Similar observations were made by dos Santos Silva et al. (2022), with *R. raciborskii* grown at 24 °C yielding higher saxitoxin production than cultures grown at 30 °C.

The effect of pH and dissolved CO<sub>2</sub> on saxitoxin production has been evaluated in *R. raciborskii* (Vilar & Molica 2020). Saxitoxin production was higher when grown in slightly acidic media (pH 6.8) or unbuffered pH compared to in alkaline media (pH 8.2). Saxitoxin was generally lower when *R. raciborskii* was provided bicarbonate as a dissolved inorganic carbon source.

#### 4.6. Summary of expected changes to cyanotoxin production with continued climate change

Understanding how climate change will impact cyanotoxin production is challenging. Many of the studies have used different culturing conditions, different methods for determining toxin concentrations, strains that live in different ambient conditions, and have variable units for normalising and presenting data. Among comparable studies, results show contrasting responses between species (e.g., microcystin-producing *Microcystis* and *Planktothrix*), and among strains of the same species (e.g., saxitoxin-producing *R. raciborskii*).

In this section we reviewed studies which explored variables closely associated with climate change. Many other variables may be indirectly related to climate change (e.g., nutrients, metal availability) and have also been shown to impact toxin production. Changes in these variables may also act synergistically with temperature and dissolved CO<sub>2</sub> concentrations. Studies evaluating multiple drivers of toxin production, e.g., the effect of temperature and light intensity, have shown complex interactions and relationships. This reinforces the difficulty in accurately predicting the impact of climate change in the natural environment.

Finally, the degree of change in toxin production observed in laboratory experiments conducted to date is generally relatively small (3- to 4-fold change in toxin quotas) and much higher changes in toxin quotas have been recorded in field experiments evaluating the effects of cyanobacteria cell density on microcystin production (18- to 362-fold change). Future work on toxin production should be conducted *in situ* to better mimic the complex interactions and multiple drivers that influence toxin production in the natural environment.

## **5. AOTEAROA NEW ZEALAND LAKES AND RIVERS UNDER CLIMATE CHANGE AND EXPECTED IMPLICATIONS FOR CYANOBACTERIA**

In this section we provide a high-level overview of the predicted impacts of climate change on lakes, streams and rivers in Aotearoa New Zealand. We then provide a detailed review of literature from this country related to climate impacts on planktonic and benthic cyanobacteria and provide a summary of likely changes under predicted scenarios.

### **5.1. Climate change and fresh water in Aotearoa New Zealand**

Continued climate change will result in higher temperatures, greater severity and frequency of floods and droughts, reduced snowfall and increases to the sea-level rise (MfE 2017). These environmental changes will reshape our freshwater environments and likely lead to an increased prevalence of toxic cyanobacteria in lakes and rivers (Figure 4). Altered rainfall patterns will result in changes to the nutrient dynamics in lakes and rivers, with increased nutrient and sediment runoff during periods of heavy rainfall and the release of bound nutrients from lake sediments during sustained dry periods. Droughts will also have an impact on river flows and groundwater and affect parts of the country differently (Hendy et al. 2018). Reduced snowfall will lower the quantity of water flowing into rivers, streams, and lakes. Higher temperatures will change the composition of flora and fauna in our freshwater ecosystems and this will not necessarily be uniform across the country (IPCC Working Group II 2022).

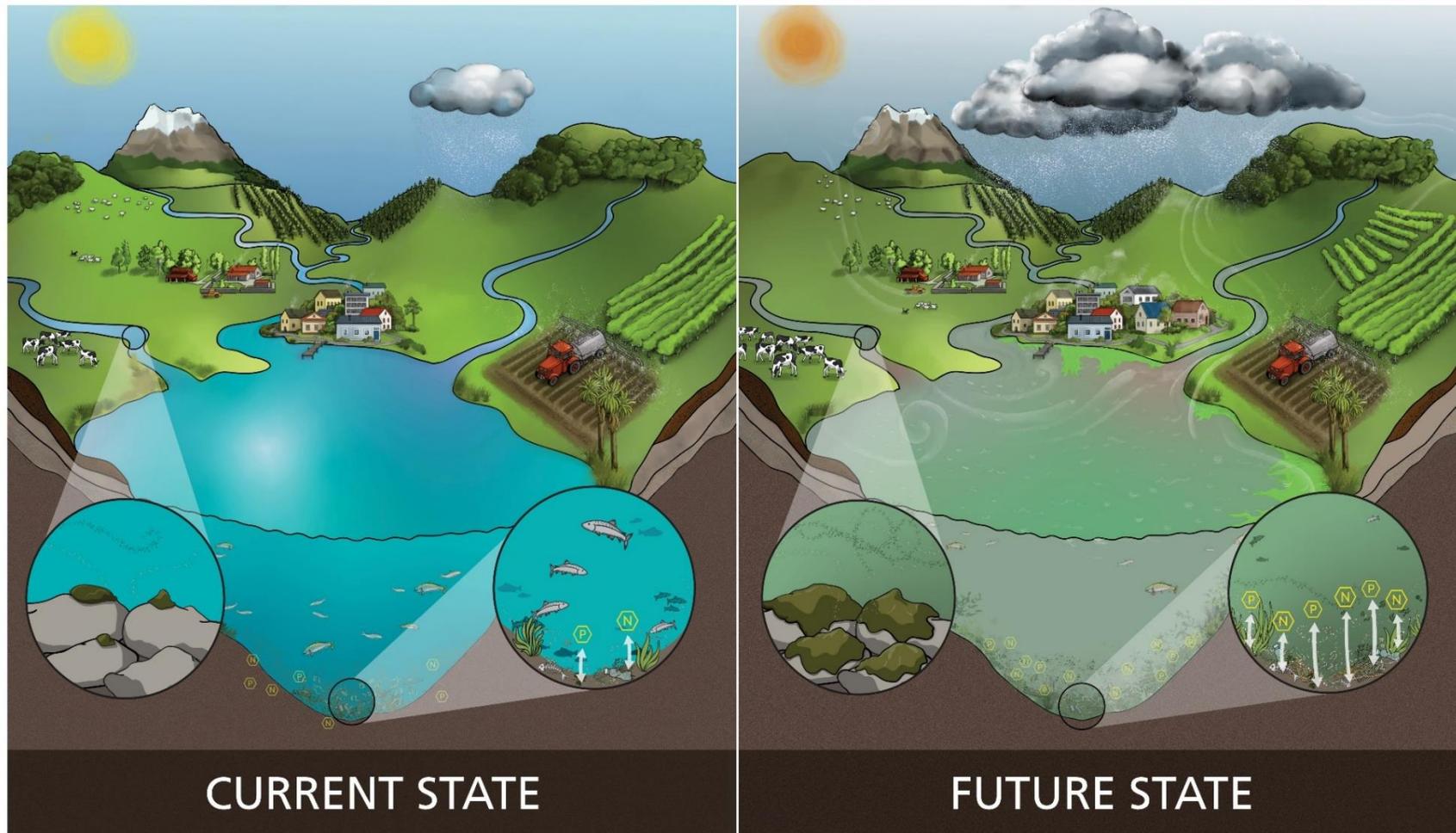


Figure 4. The current (left) and future (right) scenarios for freshwater cyanobacteria in lakes and rivers in Aotearoa New Zealand with increased eutrophication and continued climate change. Change is expected to result in more benthic cyanobacteria in rivers through increased nutrient run-off and periods of stable river flow, and more cyanobacteria in lakes due to increased run-off and the release of sediment-bound nutrients during periods of stratification. Because cyanobacteria grow better than other phytoplankton at higher temperatures, they will begin to dominate in freshwater ecosystems.

### ***5.1.1. Climate change and lakes in Aotearoa New Zealand***

A detailed review of the effects of climate change on lakes in Aotearoa New Zealand is available in Hamilton et al. (2013). They suggest the key impacts of climate change on lake health are likely to be:

- Increased temperatures, which will lead to more intense stratification and enhanced eutrophication. Rising temperature will also have a significant effect on hydrological process and ice cover in alpine systems.
- Increased precipitation in all parts of the country (except the eastern North Island and the north of the South Island), which will decrease residence times and increase external nutrient loading.
- Increased wind, which will increase turbulence and resuspension of sediment and result in a deeper mixing layer in some lakes.
- Sea level rise, which will result in the salinisation of coastal lakes and lagoons and the disappearance of some lakes.
- Changes in aquatic flora and fauna as either a direct or indirect response to climate change, including the spread and establishment of non-native species.

### ***5.1.2. Climate change and streams and rivers in Aotearoa New Zealand***

The number of hot days is projected to increase nationally both in the medium- (2031-2050) and long-term (2081-2090), with up to 70 'extra' days above 25 °C in some regions by 2090 (MfE 2018), particularly in the North Island. Changes in river / stream temperatures are likely to shift food web dynamics and favour some species over others.

As noted above, annual rainfall is expected to increase on the West Coast but decrease in the north-east of the South Island, while eastern and northern areas of the North Island will also have reduced annual rainfall (MfE 2018). Despite this, the rainfall is likely to be more intermittent with projections of less regular but more severe rain events, coupled with increases in the frequency of long dry spells. Low river / stream flow will have multiple impacts including reduction in the quantity and quality habitat for fish, invertebrates and other organisms (MfE & Stats NZ 2020). Reduced flows can also increase the concentration of nutrients and other contaminants in streams and rivers.

The impact of changing rainfall patterns on nutrient inflows in rivers / streams in Aotearoa New Zealand is not entirely clear. More intense rain events are likely to transport considerable nutrient loads into rivers / streams in strong pulses. In drier periods of low rainfall, the relative contribution of groundwater to river / stream flows increases, meaning groundwater nutrient concentrations may begin having a more significant effect on the nutrient loads during those periods. Dissolved reactive phosphorus binds to sediments, so is typically low in groundwater; however, nitrate

concentrations can be elevated in groundwater and contribute significantly to the nitrogen load in streams and rivers.

## 5.2. Review of studies that provide insights into the impacts of climate change on cyanobacteria and cyanotoxins in Aotearoa New Zealand

### 5.2.1. Planktonic cyanobacterial blooms

International research suggests that the four most common planktonic bloom-forming cyanobacterial genera observed in New Zealand (*Aphanizomenon*, *Dolichospermum*, *Microcystis* and *Raphidiopsis*) will increase in abundance as a result of climate change (O’Neil et al. 2012).

*Raphidiopsis* blooms are confined to a few large (500–300 ha) shallow (max. 5 m) North Island lakes, where they reach extremely high biomass (Wood et al. 2014a). Although drivers of these blooms are complex, the two key factors are temperature and turbidity (which are both expected to increase with climate change). Blooms usually occur only when water temperatures are above 20 °C and peak seasonal abundances correspond to summer thermal maxima (Wood et al. 2014a). Low light conditions favour *Raphidiopsis* (O’Brien et al. 2009). These lakes are highly exposed to wind and extremely turbid due to wind-driven re-suspension of fine sediment.

A 17-month study of a eutrophic lake in Aotearoa New Zealand highlighted the complexity of predicting the impacts of climate change on key bloom-forming genera (Wood et al. 2016a). The researchers investigated bloom formation and species composition in two consecutive summers with contrasting extreme weather events: intense precipitation and severe drought. In the first summer moderate levels of nitrate related to high-rainfall events and a wet summer, led to the dominance of *Aphanizomenon* and *Dolichospermum*, which either lacked or had a very low frequency of heterocytes (specialised cells which undertake nitrogen-fixation; Figure 5). *Microcystis* blooms occurred only when ammonium concentrations and water temperature increased. The extended drought in the following summer resulted in prolonged stratification, significantly higher water temperatures, increased dissolved reactive phosphorus and low dissolved inorganic nitrogen concentrations. All *Aphanizomenon* and *Dolichospermum* filaments contained heterocytes (suggesting active nitrogen-fixation) and *Microcystis* blooms did not occur (Figure 5).

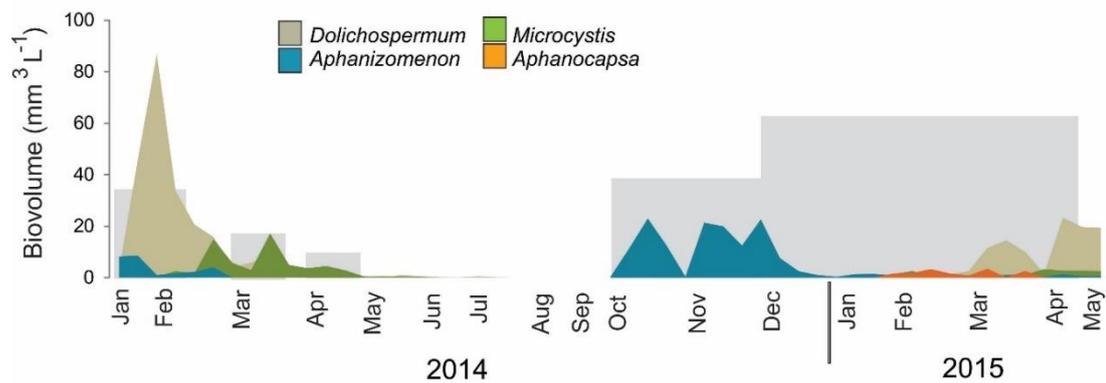


Figure 5. Cyanobacterial biovolumes in Lake Rotorua (South Island, New Zealand) over the 17-month study period (January 2014 to May 2015). Grey shading shows the presence of heterocytes and their approximate frequency (heterocyte per cell). The summer (January to April) of 2014 was characterised by frequent precipitation and two extreme rainfall events, in contrast the summer of 2014 to 2015 (October to April) had the second lowest total rainfall (over the summer period) measured since records began 75 years before present. Modified from Wood et al. (2016a).

Many bloom-forming species overwinter in lake sediment in a dormant vegetative stage or as akinetes. In spring or summer they recruit back into the water column and can provide substantial inoculum for summer blooms (Torres & Adámek 2013). Despite the relatively mild winter water temperatures in lowland lakes in Aotearoa New Zealand, benthic recruitment appears important in initiating bloom formation (Faithfull & Burns 2006; Borges et al. 2016). Although factors that promote recruitment are complex and the impacts of climate change are rarely considered in this process, research has highlighted temperature as important in shallow lakes in Aotearoa New Zealand. Laboratory studies identified temperature as one of the key triggers for *Microcystis* recruitment (Figure 6; Borges et al. 2016). Wood et al. (2014a) analysed a 10-year dataset and found that *Raphidiopsis* blooms only occurred when bottom water temperatures exceeded 22 °C, which the researchers suggested is likely related to akinete germination.

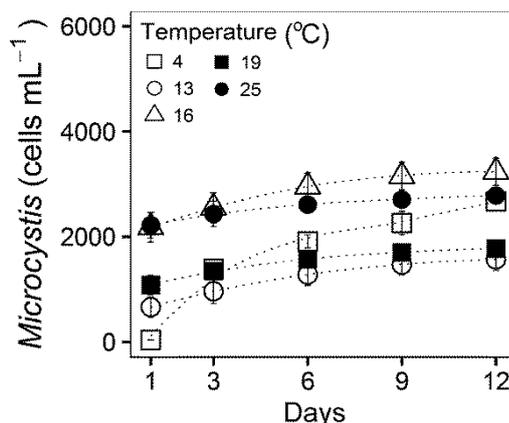


Figure 6. *Microcystis* sp. cell density over a 12-day laboratory-based experiment (data points are an average of triplicates). Surface sediment samples from Lake Rotorua (South Island, New Zealand) were incubated at five temperatures in Milli-Q water, and recruitment assessed every three days. Recruitment was significantly higher at 16 and 25 °C compared to 4, 13 and 19 °C ( $p < 0.001$ ; modified from Borges et al. 2016). Although recruitment was still observed at 4 °C, it was delayed.

Although not specifically studying cyanobacteria, several modelling studies have explored the likely impact of climate change and chlorophyll-*a* (as a proxy for total algal biomass) on lakes in Aotearoa New Zealand. Given the prevalence of cyanobacteria in the study lakes, it is a reasonable assumption that any predicted increases in chlorophyll-*a* also likely mirror cyanobacterial abundance. Me et al. (2018) investigated the impacts of nutrient load reductions and climate change on Lake Rotorua (Te Arawa lakes, Rotorua) by coupling a catchment model (SWAT) with a 1-D lake water quality model (DYRESM-CAEDYM). They found that climate change resulted in an increase in thermal stratification, which lead to greater internal nutrient loads and higher chlorophyll-*a*. They suggest that in polymictic lakes, eutrophication associated with climate change and greater internal nutrients will play a more significant role than external nutrient loading. Trolle et al. (2011), used DYRESM-CAEDYM to model the effect of climate change on three lakes. Of note were their simulations for the polymictic, eutrophic Lake Rotoehu (Rotorua region) which indicated that cyanobacteria will be more abundant in the future climate, and may increase by more than 15% in their contribution to annual mean chlorophyll-*a*.

As noted in Section 4.6, predicting how climate change will impact cyanotoxin production is challenging, as many variables appear to be involved in regulating toxin production and these differ among species, strains and geographic location (e.g., Kleinteich et al. 2012; Harke & Gobler 2013; Willis et al. 2016). Additionally, cyanobacterial blooms usually comprise both toxic and non-toxic genotypes and their relative abundance is spatially and temporally variable (Kurmayer & Kutzenberger 2003). Field studies in New Zealand suggest that within short time frames (up to 6 hours) factors not directly related to climate change cause the most dramatic changes in toxin production in *Microcystis* (Wood et al. 2011). However, a 17-month study

where genotype succession and toxin quota were investigated (Wood et al. 2016a), showed a statistically significant correlation between water temperature and microcystin quotas (Figure 7). These data indicate that predicted increases in surface water temperature may lead to higher microcystin quotas in this lake or select for toxin-producing strains which produce higher amounts of toxins.

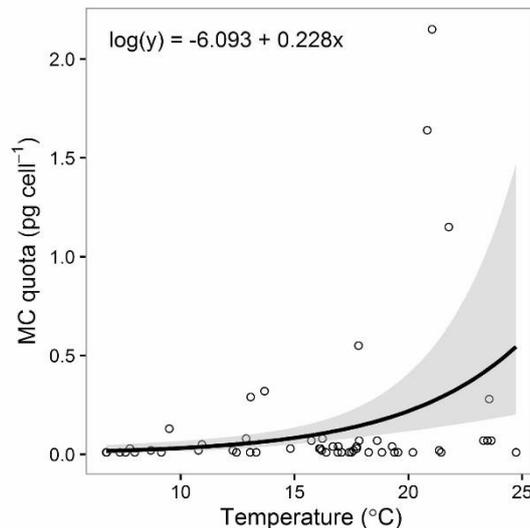


Figure 7. Univariate analysis identified a significant positive relationship ( $p < 0.001$ ) between surface water temperature and microcystin (MC) quota in a 17-month study (January 2014 to May 2015) at Lake Rotorua (South Island, New Zealand). The shaded area shows the pointwise 95% confidence interval of the fitted values. Modified from Wood et al. (2016a).

While significant attention has focused on the effect of climate change and cyanobacterial bloom formation in eutrophic lakes, less emphasis has been placed on potential shifts in cyanobacterial diversity in lakes of varying trophic status. Wood et al. (2017b) used molecular techniques to study planktonic cyanobacterial diversity in 143 lakes across Aotearoa New Zealand spanning a range of geographic, hydromorphological and trophic gradients. The authors showed that while local conditions were the most important factors in structuring community composition, geographical location (latitude, longitude and altitude) were also significant and their relative importance varied among trophic categories. Their data highlight the need to consider the broad-scale impacts that the dual effects of eutrophication and climate change will have on planktonic cyanobacteria communities.

### Future predictions

Collectively these studies indicate that cyanobacterial blooms will increase in severity and intensity. In particular, blooms will be more intense in eutrophic lakes where internal nitrogen and phosphorus cycling is a major contributor to nutrient loads. We also anticipate that the typical summer period when cyanobacterial blooms occur will

lengthen, although we note that blooms are already reported well into autumn in Aotearoa New Zealand. It is likely that the dominant cyanobacteria species will change, but predicting which taxa will become more abundant is challenging.

As subtropical areas in Aotearoa New Zealand expand southwards, there is increased potential for the spread of existing toxin-producing taxa to other parts of the country and for the introduction of new toxin-producing cyanobacteria. Examples of species or strains that might invade with warmer temperatures include those that are common in Australia, e.g., saxitoxin-producing *D. circinalis* and cylindrospermopsin-producing *R. raciborskii*. Whilst *R. raciborskii* is commonly observed in lakes in the Waikato region, toxin-producing genotypes have not been frequently observed to date. The spread of such species will rely on appropriate temperature conditions for their growth as well as a means of dispersal to new locations. Human-mediated dispersal (e.g., boats, recreational equipment, fishing gear) is the most likely vector and highlights the continued need for internal biosecurity initiatives. Dispersal of toxin-producing taxa to new waterbodies could also occur via wind-driven aerosols transporting cyanobacteria cells over short to medium distances or by birds transporting cells. Because of the wide range of growing conditions tolerated by most cyanobacteria, this 'natural dispersal' has probably already occurred. Therefore, changes to the cyanobacterial taxa observed in New Zealand waterbodies with continued climate change will likely be due to cyanobacteria already present in the waterbody becoming more abundant (i.e., going from a minor component of the community to a major component) or via human-mediated transport to newly habitable waterbodies (as described above).

### 5.2.2. Benthic proliferations in rivers and streams

The only benthic species in Aotearoa New Zealand with sufficient ecological research to allow inferences about the potential effects of climate change is *Microcoleus*. Multiple field and stream channel experiments have explored the drivers of proliferation (e.g., Wood et al. 2017a; McAllister et al. 2018a, 2018b). In general, these have highlighted an interplay between water chemistry, flow and fine sediment as the most important drivers. While these studies have not directly addressed climate change, they allow some inferences to be made. As noted above both temperature and rainfall patterns are likely to shift with climate change, impacting rivers and streams in Aotearoa New Zealand.

Wood et al. (2017a) assessed *Microcoleus* cover, physicochemical variables, and anatoxin concentrations at ten sites in seven rivers every week for two years in the Manawatū region. Using generalised additive mixed models (GAMMs) they showed that water temperature (in addition to water chemistry) had a positive and statistically significant effect on *Microcoleus* cover. The model predicted greater *Microcoleus* cover when the water temperature was  $> 15\text{ }^{\circ}\text{C}$  (Figure 8). Flow intensity in the rivers, expressed relative to the long-term median, had a positive effect up to 0.4x the median flow and a negative effect when  $> 0.5x$  the median flow (Figure 8). In a similar

study, McAllister et al. (2018a) monitored *Microcoleus* cover, physicochemical variables, and anatoxin concentrations for 30 weeks in eight rivers in Canterbury. Generalised additive mixed models identified site, month of the year, conductivity and nutrient concentrations over the accrual period as significant variables associated with *Microcoleus* cover. The effect of flow was generally consistent across rivers, with cover accruing over time since the last flushing flow. They also suggest that warmer temperatures favours the proliferation of *Microcoleus*. Neither study found any relationships between temperature and toxin content in the mats.

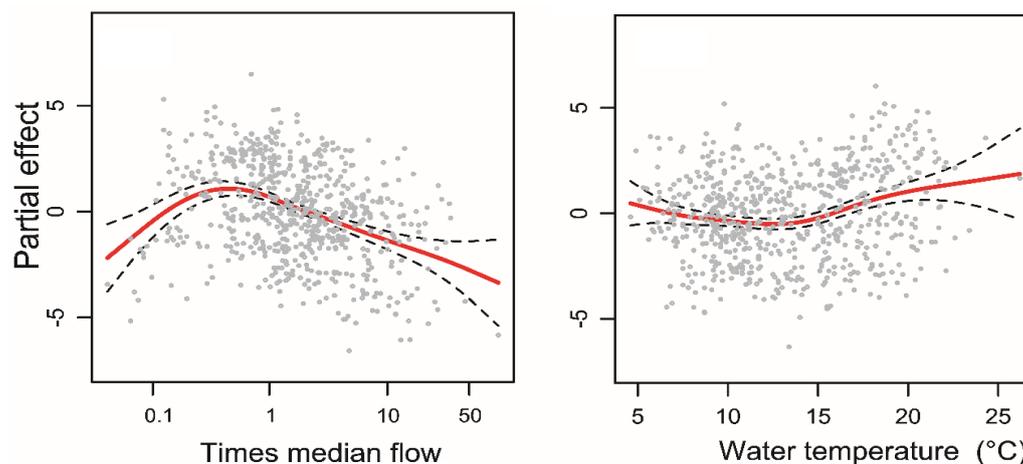


Figure 8. Partial effects plots from the generalised additive mixed models showing the effect of water temperature and flow on the percentage cover of *Microcoleus* from ten sites in seven rivers monitored every week for two years in the Manawatū region. Red lines represent cubic splines ( $\pm$  standard error, dashed black lines) fitted using a log-normal generalised additive model. Note not all variables that impacted cover are shown. Modified from Wood et al. (2017a).

Wood et al. (2020) undertook a large spatial study at 61 sites in the lower North Island over a period four years to explore drivers of *Microcoleus* proliferations. Whilst not the only driver identified, flow regime was an important predictor. Using boosted regression tree models, the authors showed that streams with a higher frequency of floods were more likely to experience *Microcoleus* proliferations. These results contrasted to the previous findings presented, and other studies (e.g., Heath et al. 2015) that indicated that prolonged stable periods allow longer accrual times, enabling more extensive proliferations. However, these results may not be mutually exclusive. Streams with a higher flood frequency may also favour *Microcoleus* proliferations because they have a growth form that adheres quite strongly to the stream substrate during initial colonisation (Hart et al. 2013; Wood et al. 2017a). This may give them a competitive advantage over other periphyton during this period. It has also been shown that *Microcoleus* can rapidly colonise bare substrate, out-competing diatoms and green algae (Brasell et al. 2015). These results add further evidence to support a nuanced response of *Microcoleus* to changes in flow regime, that are likely to be site-, river- and regionally-variable and -specific. Further research is required to tease apart

these relationships, but it seems likely that predicted changes in rainfall patterns will impact *Microcoleus* proliferations. Collectively, these data indicate that changes in river flows, as a result of variations in rainfall, will have different impacts that will vary at regional scales. It is likely that increasingly stable flows due to more intermittent, but severe, rain events will increase the accrual of *Microcoleus*, especially in regions where rainfall becomes less regular. In addition to natural changes in river flow, demand for water is increasing (particularly during summer). Direct removal of surface water reduces river flows and abstraction of groundwater will affect the interaction between river flow and groundwater storage, which may further exacerbate low-flow conditions.

Nuisance proliferations of benthic *Nostoc* and *Anabaena* are currently uncommon in Aotearoa New Zealand (although *Nostoc* is observed in our rivers, lakes and terrestrial environments). However, they may become more prevalent with continued climate change, especially in warm low-nitrate streams where their ability to fix atmospheric nitrogen would provide a significant growth advantage. Both *Nostoc* and *Anabaena* are genera known to produce a variety of cyanotoxins and could present an increasing public health risk as climatic conditions shift to favour their growth.

#### **Future predictions**

We predict that the intensity, distribution and duration of benthic proliferations of *Microcoleus* will increase in rivers and streams across Aotearoa New Zealand. This will be due to increased temperature enhancing growth rates and changes in flow regimes in rivers and streams creating conditions that are favourable for proliferation of *Microcoleus*. It is unclear how increases in storm events will impact benthic proliferations of *Microcoleus*. Intuitively, an increase in flushing flows should decrease proliferations but because of the ability of *Microcoleus* to rapidly colonise bare substrate, it may ultimately lead to higher abundances of this species in rivers and streams. To date, there is no evidence to support the idea that climate change will result in higher toxin concentrations in *Microcoleus* proliferations (per unit of *Microcoleus* biomass).

Information on all other benthic cyanobacterial species in rivers / streams (and lakes) is very limited, making it impossible to make predictions on how their abundance and composition will shift due to climate change.

#### **5.2.3. Benthic proliferations in lakes**

Research on benthic cyanobacteria in lakes has primarily focused on characterising species composition and toxin production. In the absence of any ecological data it is not possible to draw any inferences on the likely impacts of climate change on benthic cyanobacterial proliferations in lakes in Aotearoa New Zealand.

## 6. POTENTIAL RISKS TO PUBLIC HEALTH FROM TOXIC CYANOBACTERIA AND CONTINUED CLIMATE CHANGE

Many of the common bloom-forming planktonic and benthic cyanobacteria in Aotearoa New Zealand produce cyanotoxins (e.g., microcystin-producing *Microcystis* spp., nodularin-producing *N. spumigena*, cylindrospermopsin-producing *R. raciborskii*, anatoxin-producing *M. autumnalis*). Therefore, their increased prevalence and abundance will heighten the risk posed to public health through recreational activity, when consuming aquatic foodstuffs harvested from affected waterbodies, or via drinking untreated or insufficiently-treated water. With increasing temperatures, the likelihood of people visiting waterbodies for recreational purposes will also increase, further increasing the likelihood of exposure to cyanotoxins.

The result of this review shows that increased temperature can either increase the growth rate or the amount of toxin produced per cell and in *Microcystis* (a common toxin-producing cyanobacterium in Aotearoa New Zealand) higher cell densities within blooms trigger greater toxin production. Collectively this suggests that climate change will increase the levels of cyanotoxins in waterways around Aotearoa New Zealand. Higher levels of cyanotoxins will increase the health risks cyanobacteria pose to humans. Toxin concentrations can reach hazardous concentrations even when cyanobacterial biomass is low, particularly in drinking-water supplies. This is a particular concern for communities who use untreated drinking-water or regularly consume aquatic foodstuffs from contaminated waterbodies. It is likely that the current guidelines for cyanobacteria (both recreational and drinking-water) will need to be regularly evaluated to ensure that the toxin quotas used to develop thresholds are still valid, i.e., higher (or lower) levels of toxins per cell might be produced as temperatures change.

The increased prevalence and abundance of cyanobacteria and cyanotoxins with climate change may require upgrades to drinking-water treatment facilities for water supplies sourced from affected rivers, streams, lakes and reservoirs. In addition to cyanotoxins, many cyanobacteria produce taste and odour compounds such as geosmin and 2-methylisoborneol (Watson et al. 2008). Taste-and-odour compounds cause malodorous or unpalatable drinking water and aquatic foodstuffs, resulting in increased treatment costs. The monitoring costs associated with 'cyanotoxin compliance' are also likely to increase, as the presence of low levels of cyanobacteria requires higher-frequency monitoring of source waters.

In lakes and rivers that already experience problems with cyanobacteria, there will likely be more closures for recreational purposes, and this will occur for longer periods of time. The occurrence of cyanobacteria in a wider number of lakes and rivers will require more monitoring to be undertaken at times of elevated risk. Downstream

effects on rivers (from planktonic cyanobacteria) and estuaries (from both benthic and planktonic cyanobacteria) are also more likely to occur.

Because cyanotoxins can accumulate in aquatic organisms, people consuming food harvested from contaminated waterbodies are more likely to be exposed to cyanotoxins. Increased frequency and duration of recreational harvesting closures from waterbodies affected by toxic cyanobacteria will have negative health effects on people who rely on the wild-harvested food as a staple component of their diet. Because microcystins, nodularins and cylindrospermopsins also have chronic health effects (tumour promoters in the liver, and potentially other organs for cylindrospermopsins), there is the potential that long-term low-level exposure to the toxins can negatively impact human health. Epidemiological studies from China (Ueno et al. 1996; Li et al. 2011), Serbia (Svirčev et al. 2009; Svirčev et al. 2013) and USA (Zhang et al. 2015) have linked frequent low-level ingestion / consumption of microcystins to higher levels of liver cancer (above the level expected from alcohol consumption). To the best of our knowledge, similar studies have not been undertaken in Aotearoa New Zealand.

Several studies have reported microcystins / nodularins in aerosols from lakes (Backer et al. 2008, 2010; Gambaro et al. 2012; Schaefer et al. 2020), including one study from Aotearoa New Zealand (Wood & Dietrich 2011). Whilst the toxin concentrations measured in aerosols do not suggest that immediate effects to human health are likely, Plaas and Paerl (2020) identify several knowledge gaps that prevent a proper evaluation of the risk from cyanotoxin-containing aerosols. Furthermore, for people living next to waterbodies affected by toxic cyanobacteria, aerosols may provide long-term low-level exposure to cyanotoxins. As mentioned above, the long-term negative health effects from low-level cyanotoxin exposure are not well characterised.

The introduction of new toxin-producing cyanobacterial taxa to Aotearoa New Zealand poses a human health risk if they are not being monitored for under risk management frameworks. To limit this risk, recreational cyanobacterial monitoring programmes are recommended to undertake periodic checks for toxins or toxin production genes in samples containing cyanobacterial taxa that have been identified as toxin-producers overseas (often referred to as 'potential toxin-producing taxa'). Drinking-water risk management frameworks in Aotearoa New Zealand follow a conservative approach where potential toxin-producing cyanobacterial taxa trigger toxin testing of samples.

## 7. KNOWLEDGE GAPS

This review has highlighted several knowledge gaps and research opportunities:

- Internationally, and in Aotearoa New Zealand, there is a lack of knowledge on the drivers of benthic cyanobacteria proliferation in lake ecosystems. The lack of effective monitoring strategies to determine the presence and abundance of benthic cyanobacteria in lakes is a barrier to conducting research on the drivers of proliferations. Data are also lacking on the species responsible for these blooms and there is limited knowledge on toxins within the mats. Whilst several toxin-producing benthic cyanobacterial taxa have been identified in lakes of Aotearoa New Zealand, it is likely that others will be identified with wider evaluation. The development of benthic cyanobacteria monitoring strategies for lakes will not only advance research in this area but will also enable better evaluation of the human health risk when benthic cyanobacteria are identified in lakes and reservoirs used for recreational activities and drinking-water.
- Knowledge on the distribution, species composition and toxin content of cyanobacterial blooms and benthic proliferations is patchy and sporadic because no national-scale systematic surveys have been undertaken for benthic taxa in lakes, rivers and streams, and key data are missing from surveys of planktonic species. While many regional councils collect samples from lakes for cyanobacterial species identification and enumeration or undertake visual surveys for benthic cyanobacteria in rivers and streams, toxin analysis is rarely undertaken. In the case of benthic cyanobacteria in rivers and streams, no taxonomic evaluation is undertaken. This limits our ability to make accurate national-scale evaluations of the current health risks posed by cyanobacteria and their toxins.
- Empirical data on how storms and droughts impact cyanobacteria in lakes are lacking. Automatic high-frequency monitoring platforms have been installed in 18 lakes in Aotearoa New Zealand and have collected continuous high-frequency temperature, chlorophyll-*a*, dissolved oxygen and turbidity data for long periods of time (more than 10 years for some lakes). Using statistical approaches, these data, in concert with meteorological information, could provide valuable insights into short-term (i.e., intra-annual time scales) responses to extreme climate events. Additionally, cyanobacterial monitoring data collected by regional councils could also provide insights into the response of cyanobacteria to storms, droughts, and other recurring climate patterns such as the El Niño-Southern Oscillation. A caveat with this analysis is that these data have been collected for the purpose of protecting recreational water users, rather than monitoring long-term ecological patterns, thus caution will be needed when interpreting the results.
- Empirical data on how storms and droughts will impact cyanobacteria in rivers are lacking. Some regional councils have been monitoring benthic *Microcoleus* proliferations since c. 2010. This may provide an avenue to explore the impact of storm events or droughts in rivers that have a flow gauge. Our previous attempts

to undertake this type of analysis has proved challenging as often data are not collected when levels of *Microcoleus* are low (< 20%), and it is deemed there is no health risk. Establishing several long-term sites where more rigorous monitoring was undertaken could allow insight into how benthic cyanobacterial proliferations in rivers and streams respond to extreme weather events.

- A range of lake ecosystem models exist that allow the effect of climate change (and other stressors) on planktonic cyanobacteria to be predicted. Similar approaches are not available for benthic cyanobacteria (e.g., *Microcoleus*) in rivers. Further efforts might be directed towards continuing the development of mechanistic models that can predict the occurrence of *Microcoleus*. Preliminary site-specific mechanistic models have been developed for two rivers in Southland (Atalah et al. 2018). With additional development and validation, this modelling approach could be useful for predicting how *Microcoleus* cover is likely to change under differing temperature and flow regimes.
- In the area of cyanotoxin accumulation in aquatic foodstuffs there are several knowledge gaps that make evaluating the human health risk difficult:
  1. Whilst the accumulation of some cyanotoxins is well researched in a range of aquatic foodstuffs (cylindrospermopsins, microcystins, saxitoxins), the bioaccumulation of anatoxins in food webs has not been widely investigated.
  2. Knowledge on cyanotoxin concentrations in aquatic foodstuffs is limited to several studies conducted in distinct locations over fixed periods of time. Regular monitoring programmes would provide greater knowledge on the levels of cyanotoxins in aquatic foodstuffs throughout Aotearoa New Zealand. These data will be useful for determining 'allocation factors' (the level of toxin exposure expected from different sources; recreational activity, food, drinking-water) when calculating alert-level thresholds for risk management frameworks.
  3. To assist with risk assessments, knowledge on the consumption rates of wild-harvested aquatic foodstuffs in Aotearoa New Zealand could be extended. Studies have been undertaken in South Canterbury (Arowhenua; Tipa et al. 2010a), Rotorua lakes (Te Arawa; Tipa et al. 2010b) and Northland (only shellfish consumption was evaluated; Guy et al. 2021), but the current data would be strengthened by undertaking surveys in additional regions.
  4. Health-based guidance values for safe levels of cyanotoxins in aquatic foodstuffs have not been established in Aotearoa New Zealand (to the best of our knowledge). The information from Point 3 above would prove useful for this.
  5. There is a lack of knowledge on whether regular low-level exposure to cyanotoxins with chronic health effects (i.e., microcystins, nodularins and cylindrospermopsins) have had negative health effects on people in

Aotearoa New Zealand. In this country, microcystins and nodularins ingested through mahinga kai consumption and potentially inhalation are the most relevant route for investigation here due to their prevalence in Aotearoa New Zealand, their accumulation in aquatic foodstuffs and strong evidence that the toxins act as liver tumour promoters.

- It is likely that climate change will necessitate more cyanobacteria monitoring to be undertaken (because more waterbodies are affected and because blooms and proliferations are in waterbodies present for longer). Rethinking and modernising how cyanobacteria monitoring in Aotearoa New Zealand is undertaken would allow larger scale monitoring programmes and more rapid results. The incorporation of technologies such as field-portable fluorometers (Thomson-Laing et al. 2020) and unmanned aerial vehicles (i.e., drones; Biggs et al. 2021) are examples that might improve the efficiency and turnaround of monitoring programmes. However, further validation and evaluation of the limitations of these techniques is required before they can be incorporated into risk management frameworks for the protection of human health.

## 8. CONCLUSIONS

This review provides evidence that suggests the intensity, duration and distribution of planktonic cyanobacterial blooms in lakes and reservoirs, and benthic proliferations in rivers, streams and lakes in Aotearoa New Zealand will increase with climate change. There is less clarity as to whether there will be a corresponding increase in the amount of cyanotoxin produced per cell. However, because the blooms and proliferations are likely to be more intense, persist for longer and occur in more lakes, rivers and streams there will be increased likelihood of human exposure to cyanotoxins. This exposure will occur via recreational activities (contact with skin, accidental consumption of water and through aerosols), drinking-water (when there is inadequate water treatment undertaken), and via the consumption of aquatic foodstuffs sourced from contaminated water bodies.

To reduce risks there is a need for more knowledge on:

- the occurrence of cyanobacteria and cyanotoxins in lakes and rivers (both planktonic and benthic)
- how extreme weather events, in particular storms and droughts, will affect cyanobacterial species
- cyanotoxin accumulation in aquatic foodstuffs.

There is also a need to enhance our ability to predict how benthic cyanobacteria will respond to climate change and to improve cyanobacterial monitoring programmes so that they capitalise on new technology. It will not be possible to monitor all waterbodies and there is a need for ongoing educational initiatives to ensure that the public can make informed decisions about the risk associated with cyanobacteria.

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