



Spatiotemporal dynamics of *Phormidium* cover and anatoxin concentrations in eight New Zealand rivers with contrasting nutrient and flow regimes



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HIGHLIGHTS

- In New Zealand, toxic *Phormidium* proliferations are a major concern due to their increasing extent and severity.
- Our aim was to advance understanding of variables associated with high *Phormidium* cover and toxin concentrations.
- We measured *Phormidium* dynamics, toxins and physicochemical variables weekly for 30 weeks in eight New Zealand rivers.
- Multiple factors, including, the specific site, water chemistry and time of the year influenced *Phormidium* accrual.
- This highlights the difficulty in developing a robust prediction tool and a meaningful region-wide management programme.

GRAPHICAL ABSTRACT



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ABSTRACT

Toxic benthic cyanobacterial proliferations, particularly of the genus *Phormidium*, are a major concern in many countries due to their increasing extent and severity. The aim of this study was to improve the current understanding of the dominant physicochemical variables associated with high *Phormidium* cover and toxin concentrations. *Phormidium* cover and anatoxin concentrations were assessed weekly for 30 weeks in eight predominately cobble-bed rivers in the South Island of New Zealand. *Phormidium* cover was highly variable both spatially (among and within sites) and temporally. Generalized additive mixed models (GAMMs) identified site, month of the year, conductivity and nutrient concentrations over the accrual period as significant variables associated with *Phormidium* cover. Cover was greatest under low to intermediate accrual dissolved inorganic nitrogen (DIN) and dissolved reactive phosphorus (DRP) concentrations. Accrual nutrients had a strong, negative effect on cover at concentrations $> 0.2 \text{ mg L}^{-1}$ DIN and 0.014 mg L^{-1} DRP. The effect of flow was generally consistent across rivers, with cover accruing with time since the last flushing flow. Total anatoxins were detected at all eight study sites, at concentrations ranging from 0.008 to 662.5 mg kg^{-1} dried weight. GAMMs predicted higher total anatoxin concentrations between November and February and during periods of accrual $\text{DRP} < 0.02 \text{ mg L}^{-1}$. This study suggests that multiple physicochemical variables may influence *Phormidium* proliferations and also

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1. Introduction

Toxic planktonic cyanobacterial blooms have been described for many decades (Francis, 1878; Hallegraef, 1993; Wynne et al., 2010). This has resulted in many studies investigating the physicochemical factors influencing the growth and proliferation of planktonic species (see Oliver et al., 2012). In contrast, toxic benthic proliferations are a more recent but escalating problem in freshwater environments worldwide (Quiblier et al., 2013). Toxin-producing species belonging to the genus *Phormidium*, have a cosmopolitan distribution and are found in a variety of benthic habitats including eutrophic and oligotrophic lakes, many ponds and in oligotrophic lotic systems (Komárek, 1999; Mez et al., 1998; Puschner et al., 2008; Wood et al., 2012a, 2016). In New Zealand's cobble-bed rivers, *Phormidium* proliferations (defined as >20% cover) have become increasingly prevalent over the last decade and have been identified in >100 rivers nationwide (McAllister et al., 2016). A recent study of wadeable streams in California (USA) also detected *Phormidium* species in over a third of sites sampled (Fetscher et al., 2015).

Although benthic algae, including cyanobacteria, are an important component of river ecosystems, excessive biomass and dominance by toxin-producing species can be problematic. Knowledge on the drivers of such proliferations is essential for effective management. Light, nutrient supply, hydrological regime and temperature are thought to be the most important abiotic factors determining benthic algal biomass accrual dynamics in lotic systems (Bowman et al., 2007; Clausen and Biggs, 1997; Dodds et al., 2002; Schiller et al., 2007). Non-linear responses to these variables and interactions can be expected, for example Biggs et al. (1998) suggested that, under oligotrophic conditions, increasing flow enhances accrual by increasing the flux of nutrients to the algae by reducing the thickness of the diffusive boundary layer, but that this effect is less evident at high ambient nutrient concentrations (Biggs et al., 1998; Biggs and Hickey, 1994; Borhardt, 1994). As velocity increases, however, greater shear stress can lead to enhanced sloughing and biomass reduction regardless of nutrient status (Biggs and Thomsen, 1995). *Phormidium*-dominated (hereafter referred to as *Phormidium*) mats, however, are functionally different, due to their thick, cohesive growth form. In particular it has been shown that biogeochemical conditions, including nutrient concentrations, within the mats can be very different from the overlying water (Wood et al., 2015) and it is thus uncertain whether water-derived nutrients that promote periphyton growth in general are equally relevant to *Phormidium* mats.

Only recently has research begun to explore relationships between physicochemical variables and *Phormidium* dynamics. Schneider (2015) found, in a long-term study of two Norwegian rivers, that *Phormidium* cover increased with rising annual temperatures, but decreased with prolonged high flow events. Similarly, Heath et al. (2011) observed highest *Phormidium* cover at sites in the Hutt River (New Zealand), when river flows were stable and water temperatures elevated. Heath et al. (2011) noted that there was no correlation between water-column nutrients and *Phormidium* cover, although nutrient samples were only collected monthly. In contrast, in a multi-site investigation Wood et al. (2017) indicated that *Phormidium* proliferations predominantly occurred at sites with low dissolved reactive phosphorus (DRP; ca. <0.005 mg L⁻¹) and dissolved inorganic nitrogen (DIN) concentrations of <0.8 mg L⁻¹. They also found that increasing conductivity and temperature were associated with higher *Phormidium* cover.

Species of *Phormidium* are known to produce a variety of cyanotoxins including; anatoxin-a (ATX), homoanatoxin-a (HTX), dihydro-anatoxin-a (dhATX) and dihydro-homoanatoxin-a (dhHTX; Faassen et al., 2012; Fetscher et al., 2015; Gugger et al., 2005; Heath et al., 2010; Wood et al., 2007). *Phormidium* has been implicated in animal toxicosis events in France, Netherlands, New Zealand, Scotland, Switzerland and the United States of America (Edwards et al., 1992; Faassen et al., 2012; Gugger et al., 2005; Hamill, 2001; Mez et al., 1997; Puschner et al., 2008; Wood et al., 2007). The effects of *Phormidium* proliferations on ecosystem health and aquatic organisms are largely unknown. In Spanish streams, toxic benthic cyanobacterial mats have been associated with decreased macroinvertebrate diversity (Aboal et al., 2000, 2002). Despite the apparent health risk and potential ecosystem effects, few studies have investigated relationships between toxin concentrations within mats and physicochemical variables.

Phormidium mats vary substantially in their toxin content both spatially and temporally (Heath et al., 2010; Wood et al., 2007). This variability is likely to be at least partially explained by the presence of both non-toxic and toxic genotypes, which co-occur within mats (Wood et al., 2010, 2012b). Wood et al. (2012b) found that anatoxin concentrations varied 100-fold between *Phormidium* strains isolated from the same mat and that there were differences in the 16S ribosomal RNA gene sequences of at least 17 nucleotides between anatoxin and non-anatoxin producing strains. The abundance of different strains may therefore also influence the toxin content of a mat. Both observational-based and culture-based laboratory studies have begun to explore factors that regulate the abundance of non-toxic and toxic strains and the amount of anatoxin produced. Heath et al. (2011) suggested temperatures exceeding 13.4 °C favor toxic over non-toxic strains. However, subsequent studies have found no relationship between water temperature and toxin concentrations (Wood et al., 2017). They suggested that understanding the relationships between physicochemical factors and toxin concentrations could be enhanced through the development of molecular techniques, which would allow differentiation of toxic and non-toxic strains.

In the present study we surveyed *Phormidium* weekly for 30 weeks, at a single site on eight rivers in the Canterbury region in New Zealand. The aims were to describe the spatial and temporal variability of *Phormidium* cover and total anatoxin concentrations and to investigate relationships between physicochemical variables and *Phormidium* cover and total anatoxin concentrations in the mats. The following hypotheses were tested: (1) water chemistry plays a significant role in determining *Phormidium* cover; (2) as river flow decreases, *Phormidium* cover will increase; and (3) there will be no relationships between total anatoxin concentrations in the mats and measured physicochemical variables.

2. Materials and methods

2.1. Study area and site selection

All study sites were located within the Canterbury region in the South Island of New Zealand, where catchment land-use is dominated by intensive agriculture (Table 1). A single site on each of the eight predominately gravel and cobble-bed rivers were chosen for this study (Fig. 1). Sites were selected to include areas with and without historical records of *Phormidium* proliferations. Catchment land-use data were retrieved from the Freshwater Ecosystems of New Zealand (FENZ)

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