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Review

The rise of toxic benthic *Phormidium* proliferations: A review of their taxonomy, distribution, toxin content and factors regulating prevalence and increased severity

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ABSTRACT

There has been a marked increase in the distribution, intensity and frequency of proliferations of some species of the benthic mat-forming, toxin-producing genus *Phormidium* in rivers globally over the last decade. This review summarises current knowledge on their taxonomy, distribution, toxin content, environmental drivers of proliferations, and monitoring and management strategies in New Zealand. Although toxic *Phormidium* proliferation occurs in rivers worldwide little is known about these factors in most countries. Proliferations, defined as >20% cover of a riverbed, have been identified in 103 rivers across New Zealand. Morphological and molecular data indicate the main species responsible is *Phormidium autumnale*. In New Zealand *Phormidium* produces anatoxins (anatoxin-a, homoanatoxin-a, dihydroanatoxin-a, and dihydrohomoanatoxin-a) and these were detected in 67% of 771 samples from 40 rivers. The highest concentration measured was 712 mg kg^{-1} dried weight (Oreti River, Southland), with considerable spatial and temporal variability in anatoxin concentrations between and within rivers. A synthesis of field based studies suggests that *Phormidium* proliferations are most likely when there is some enrichment of dissolved inorganic nitrogen but when water-column dissolved reactive phosphorus is less than 0.01 mg L^{-1}. Once established *Phormidium*-dominated mats trap sediment and internal mat biogeochemistry can mobilise sediment-bound phosphorus, which is then available for growth. Removal of *Phormidium*-dominated mats is primarily due to shear stress and substrate disturbance, although there is also evidence for autogenic detachment. A combination of factors including; changes to riparian margins, increased nitrate and fine sediment loads, and alterations in flow regimes are likely to have contributed to the rise in *Phormidium* proliferations.

Contents

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1. Introduction

The filamentous cyanobacterial genus *Phormidium* (Fig. 1A) is cosmopolitan and is found in diverse habitats including; intertidal marshes, alpine streams, thermal springs, and Arctic and Antarctic lakes (Broady and Kibblewhite, 1991; Quesada et al., 1999; Komárek and Anagnostidis, 2005). Under favourable hydrological and environmental conditions, *Phormidium* forms cohesive mats which can cover large areas of substrate (Fig. 1B–D). Expansive *Phormidium* mats have been recorded in both oligotrophic and eutrophic environments (Mez et al., 1998; Komárek, 1999; Wood et al., 2012a). Although dominated by *Phormidium*, these mats also contain a plethora of other organisms including bacteria, other cyanobacteria, and to a lesser extent eukaryotic algae (Hart et al., 2013; Brasell et al., 2015). These consortia of micro-organisms often benefit each other physiologically, and are bound together, and to the substrate, by extracellular polymeric substances (EPS). Hereafter these microbial communities are collectively referred as *Phormidium*-dominated mats. These mats also contain inorganic matter, including sediment (Fig. 1B; Wood et al., 2015b).

Species belonging to the genus *Phormidium* can produce a range of cyanotoxins (Gugger et al., 2005; Teneva et al., 2005; Wood et al., 2007; Borges et al., 2015). The most commonly produced toxins are the powerful neuromuscular-blocking anatoxin-a (ATX) and homoanatoxin-a (HTX) and their structural derivatives (Quiblier et al., 2013). Animal deaths linked to ingestion of microbial mats containing anatoxin producing *Phormidium* species have been reported in France, Netherlands, the United States of America, and New Zealand (Gugger et al., 2005; Wood et al., 2007; Puschner et al., 2008; Faassen et al., 2012). In France, ingestion of mats dominated by ATX-producing *Phormidium favosum* were implicated in the rapid death of two dogs at the Loue River (Gugger et al., 2005). A similar event occurred in Netherlands, where three dogs died at Lake IJmeer after ingesting mats containing *Phormidium* and high concentrations of ATX (Faassen et al., 2012).

Over the last decade there has been an apparent increase in the prevalence of benthic *Phormidium* proliferations (defined as >20% coverage of the benthos by *Phormidium*-dominated mats) in some New Zealand rivers (Heath, 2009). The first documented animal toxicosis event due to ingestion of benthic cyanobacteria occurred in 1998 in the Waikanae River (lower North Island), where five dogs died in three days (Hamill, 2001). Using a mouse bioassay and high-performance liquid chromatography with fluorescence detection (HPLC-FLD) the presence of natural degradation products of ATX was subsequently confirmed in a benthic mat dominated by *Oscillatoria*-like species (Hamill, 2001). Further sudden deaths of dogs were reported at the Mataura River (lower South Island) in 1999 and 2000. Benthic *Oscillatoria*-like mats were collected and their toxicity confirmed by mouse bioassay (Hamill, 2001).

In November 2005, at least five dogs died rapidly after visiting the Hutt River (lower North Island). Extensive benthic mats dominated by *Phormidium autumnale* were found in the river (Wood et al., 2007). Liquid chromatography–mass spectrometry (LC–MS) analysis of the mats and the stomach contents from a

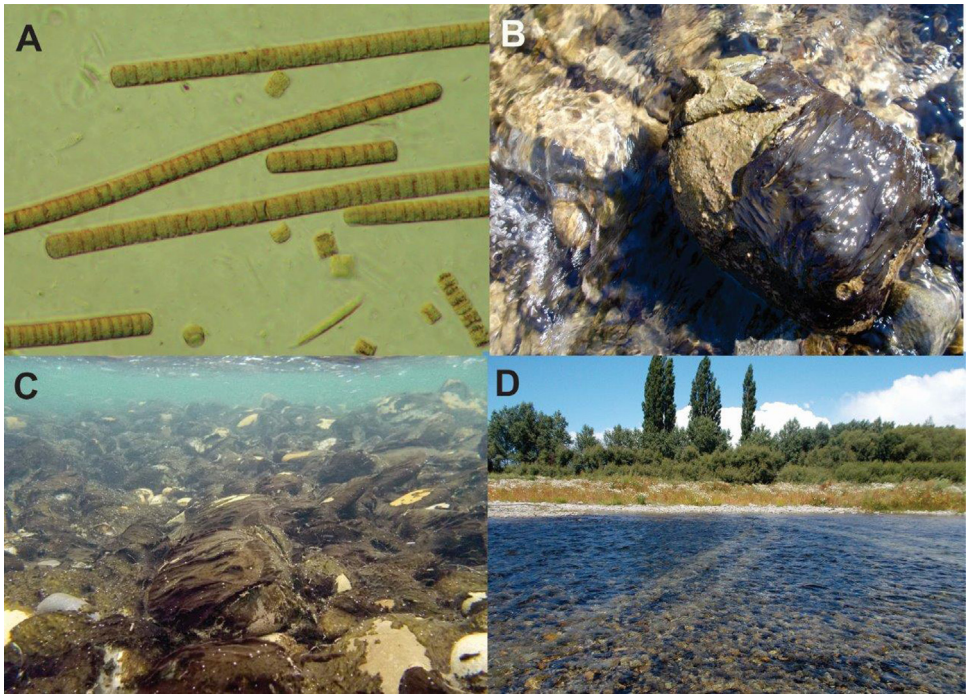

Fig. 1. (A) Example of typical *Phormidium* filament observed in *Phormidium*-dominated mats in New Zealand. This filament was from the study of Wood et al., 2007 (Hutt River, Wellington, New Zealand), (B) a thick *Phormidium*-dominated mat from the Selwyn River (New Zealand), the left-hand side of the mat has been peeled back to show the layer of fine sediment commonly observed at the mat-rock interface, and (C, D) *Phormidium* proliferations in the Opihi River (New Zealand).