

A paleoecological investigation of recent cyanobacterial blooms and their drivers in two contrasting lakes

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ABSTRACT

Cyanobacterial blooms are one of the most significant threats to global water security and freshwater biodiversity. Interactions among multiple stressors, including habitat degradation, species invasions, increased nutrient runoff, and climate change, are key drivers. However, assessing the role of anthropogenic activity on the onset of cyanobacterial blooms and exploring response variation amongst lakes of varying size and depth is usually limited by lack of historical records. In the present study we applied molecular, paleolimnological (trace metal, Itrax- μ -XRF and hyperspectral scanning, chronology), paleobotanical (pollen) and historical data to reconstruct cyanobacterial abundance and community composition and anthropogenic impacts in two dune lakes over a period of up to 1200 years. Metabarcoding and droplet digital PCR results showed very low levels of picocyanobacteria present in the lakes prior to about CE 1854 (1839–1870 CE) in the smaller shallow Lake Alice and CE 1970 (1963–1875 CE) in the larger deeper Lake Wiritoa. Hereafter bloom-forming cyanobacteria were detected and increased notably in abundance post CE 1984 (1982–1985 CE) in Lake Alice and CE 1997 (1990–2007 CE) in Lake Wiritoa. Currently, the magnitude of blooms is more pronounced in Lake Wiritoa, potentially attributable to hypoxia-induced release of phosphorus from sediment, introducing an additional source of nutrients. Generalized linear modelling was used to investigate the contribution of nutrients (proxy = bacterial functions), temperature, redox conditions (Mn:Fe), and erosion (Ti:Inc) in driving the abundance of cyanobacteria (ddPCR). In Lake Alice nutrients and erosion had a statistically significant effect, while in Lake Wiritoa nutrients and redox conditions were significant.

1. Introduction

Many lakes and their catchments have experienced intense habitat degradation, species invasions, and pollution, resulting in widespread eutrophication (Adrian et al., 2009; McCrackin et al., 2017; Jane et al., 2021). Cyanobacteria often proliferate in these conditions and the resulting blooms are a major water quality threat (Brooks et al., 2016). Cyanobacterial blooms can have significant negative ecological

consequences, including oxygen depletion and declining aquatic biodiversity (Huisman et al., 2018) and many bloom-forming species produce cyanotoxins. These pose health risks to humans and animals through ingestion or contact, which can result in poisoning, disease, and potential long-term health effects (Paerl and Otten 2013).

Cyanobacterial blooms are increasing in frequency, intensity, and duration worldwide (Reissig et al., 2006; Beaulieu et al., 2013). Environmental changes, such as rising water temperatures, extended

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stratification periods and increased severity of weather events further exacerbate the occurrence of blooms (Paerl and Paul 2012). Understanding and delineating the importance of different drivers in relation to other lake attributions is crucial for guiding the development of effective and efficient mitigation strategies. The significance of each driver varies among lakes, and understanding and delineating their importance is crucial for guiding the development of effective mitigation strategies. There is limited knowledge on whether lakes that differ in size but experience similar stressors vary in their susceptibility to cyanobacterial blooms.

Historical lake monitoring records are scarce in most parts of the world, and monitoring programs typically commence after lakes have degraded significantly. This makes it challenging to determine when and why cyanobacterial blooms initiated in a specific lake. Paleolimnology offers a valuable approach for reconstructing the historic conditions of a lake and its catchment. Until recently, methods for reconstructing biological communities have been limited to taxa that leave microfossils or biomarkers in the sediment (Mills et al., 2018), but the advent of environmental DNA (eDNA) techniques enables the composition of soft-celled, micro-, and macro-organisms in sediment cores to be investigated (Barouillet et al., 2023). Recent research has demonstrated the successful use of sedimentary ancient DNA (sedaDNA) to reconstruct historical lake biodiversity across a broad spectrum of organisms (Barouillet et al. 2022). An increasing number of studies have used sedaDNA to explore historical shifts in cyanobacterial abundance and / or composition and shown congruence between historical monitoring data (Monchamp et al., 2016; Mejbel et al., 2022) and traditional paleolimnological approaches, such as pigment inferences (Picard et al., 2022b; Erratt et al., 2023a).

The environmental history of Aotearoa New Zealand provides a unique opportunity for applying sedaDNA to paleolimnology to investigate the impact of anthropogenic activities on the onset and intensification of cyanobacterial blooms. A prehuman reference condition can be established because the first humans, Māori (indigenous people of Aotearoa New Zealand), only arrived about 750 years ago. As Māori

settled, native forest was reduced in many regions in some cases for subsistence agriculture, and mammals (rats and dogs) were introduced (McGlone and Wilmshurst 1999; Parkes and Murphy 2003). European settlers arrived in the early 1800s CE, further reducing native vegetation, establishing small-scale low-intensity farms (MacLeod and Moller 2006), and introducing non-native mammals and freshwater fish (Parkes and Murphy 2003). By the early 1900s, European farming practices intensified, with larger-scale farms and the adoption of techniques such as phosphate-based fertilizer application (MacLeod and Moller 2006).

In this study we used genetic markers to reconstruct cyanobacterial abundance and species composition in two lakes in the same landscape and land-use regime in Aotearoa New Zealand. The objectives of this study were to: (1) determine if the onset of cyanobacterial blooms was synchronous among two lakes of differing area and depth; and (2) explore how cyanobacterial abundance and composition changed over time with increasing human impact. Exploring the onset and subsequent intensification of cyanobacterial blooms in contrasting lakes will help guide the development of more effective and lake-specific mitigation strategies.

2. Materials and methods

2.1. Study sites

Lakes Alice and Wiritoa are dune-formed lakes in the Manawatū-Whanganui region of Aotearoa New Zealand (Fig. 1). Lake Alice is shallow (3.2 m max. depth) with a surface area of 12 ha. Lake Wiritoa has about twice the area (22 ha) and is relatively deep for a dune lake in this region (19.5 m max. depth). The catchments feeding Lake Alice (238 ha) and Wiritoa (696 ha) are both dominated by exotic high producing pasture (69 % Lake Alice, 71 % Lake Wiritoa; Fig. 1). Both lakes now experience cyanobacterial blooms every summer and routine monitoring shows Lake Alice is supertrophic and Lake Wiritoa eutrophic (LAWA 2023).

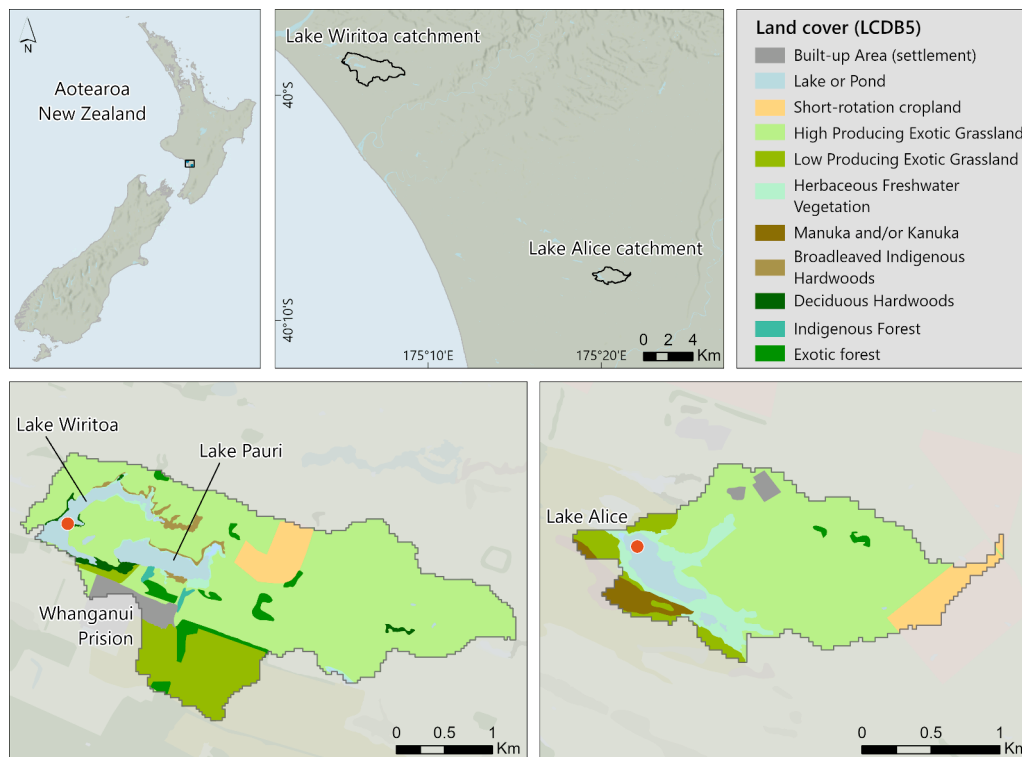


Fig. 1. Location, current land use and coring sites (red dot) of lakes Alice and Wiritoa in Whanganui, New Zealand. Land use data from the Landcover Database version 5.0 (LCDB5) from Landcare Research New Zealand Ltd.

Estimates for total, long term (steady-state) 'loads to lake' for phosphorus and nitrogen have been modelled using Catchment Land Use for Environmental Sustainability model (CLUES; Woods et al., 2006) and these data have been retrieved from takiwa.co. Lake Alice has an areal total phosphorus load of $0.37 \text{ kg ha}^{-1}\text{y}^{-1}$ and an areal total nitrogen load of $8.63 \text{ kg ha}^{-1}\text{y}^{-1}$ and Wiritoa $0.05 \text{ kg ha}^{-1}\text{y}^{-1}$ and $1.51 \text{ kg ha}^{-1}\text{y}^{-1}$, respectively. Water column profiles of temperature and dissolved oxygen are not available for Lake Alice but its shallow depth suggests regular prolonged stratification is unlikely. In contrast, Lake Wiritoa shows seasonal stratification and hypolimnetic deoxygenation (Waters et al., 2017).

Details of the environmental history of the lakes were obtained from peer-reviewed publications, technical reports, news media, and historical accounts.

2.2. Sediment core collection and chronology

Lakebed sediment cores were collected at Lake Alice (115 cm) and Lake Wiritoa (165 cm) on 31 and 29 July 2020, respectively. The cores were taken from the depocenter using a Uwitech gravity corer (Mondsee, Austria) with a 2 m-long, 90 mm diameter polyvinyl chloride core barrel that had been pre-sterilised (2 % bleach). The core was split and subsampled at Te Pū Ao / GNS Science in Wellington, Aotearoa New Zealand. One half of the core was subsampled for chronology, pollen, metals, and DNA analyses following the methods described in Short et al. (2022). The other half of the core was used for hyperspectral and X-ray fluorescence (XRF) scanning.

Macrofossil samples (Alice $n = 1$, Wiritoa $n = 7$) selected for ^{14}C dating were cleaned of residual sediment under a dissecting microscope and treated to remove carbonates, fulvic and humic compounds using an acid-alkaline-acid pre-treatment (Norris et al., 2020). Macrofossils were converted to CO_2 by combustion, graphitized and measured by accelerator mass spectrometry at the Rafter Laboratory (Wellington, Aotearoa New Zealand; Baisden et al., 2013). The Southern Hemisphere calibration curve 1 (SHCal20) was used to convert Conventional Radiocarbon Ages (CRA) to calendar years (Hogg et al., 2020).

Unsupported ^{210}Pb ($^{210}\text{Pb}_{\text{ex}}$) analysis was undertaken on 14 Lake Alice samples and 15 Lake Wiritoa samples (Supplementary Table 1 and 2). Sediment samples underwent chemical extraction and alpha spectrometry to measure ^{210}Pb at the ESR National Centre for Radiation Science (Christchurch, Aotearoa New Zealand). Supported ^{210}Pb was estimated using the asymptote of the ^{210}Pb decay profile with core depth and $^{210}\text{Pb}_{\text{ex}}$ calculated by subtracting unsupported from total ^{210}Pb . The $^{210}\text{Pb}_{\text{ex}}$ data was modelled with the piecewise Constant Rate of Supply (CRS) model in the R package Serac (Bruel and Sabatier 2020) and was constrained by bomb spike ^{14}C measurements calibrated with the Bomb21 SH12 calibration curve (Hua et al., 2022). The models used dry sediment mass calculated from computed tomography (CT) densitometry. CT data was also used to calculate bulk density of sediment using Ashi (1993) relationship between CT and bulk density. Independent age estimates derived from bomb spike ^{14}C ages and the first occurrence of exotic *Rumex acetosella* pollen were used to validate the $^{210}\text{Pb}_{\text{ex}}$ age model.

Age-depth modelling used a Bayesian framework in OXCAL 4.4 (Bronk Ramsey 2009). The $^{210}\text{Pb}_{\text{ex}}$ age-depth model, pollen biostratigraphy and calibrated ^{14}C dates were used to generate probability density functions that were then integrated with core depth using the P_Sequence prior model with a variable event thickness constant k (Bronk Ramsey 2008; Bronk Ramsey and Lee 2013).

2.3. Pollen analysis

Pollen extraction and analysis followed standard methods (Bennett 1989). Pollen and spore identifications were made using standard texts (Pocknall 1981a, 1981b, 1981c; Moar 1993) and Aotearoa New Zealand reference collections. Data are presented as relative frequency of a

minimum pollen sum of 150 grains. This sum includes pollen from all dryland plants: trees, shrubs and herbaceous plants, and non-native plant taxa. Bracken fern or rahurahu (*Pteridium esculentum*) is included in the dryland pollen sum because its functional morphology is closer to a shrub than a typical fern and a stand is ecologically equivalent to shrubland in a post-disturbance Aotearoa New Zealand landscape (McGlone et al., 2005). Pollen and spores of other groups (wetland, aquatics, ferns, tree ferns and non-palynomorphs) were excluded from the sum, but their percentages were calculated as a proportion of dryland pollen, plus the respective group. Charcoal abundance (# per cm^{-3}) was calculated from the number of charcoal fragments counted in pollen samples.

Pollen data were used to delineate human occupation periods. Increased bracken fern was used as a chronological marker for the first presence of Māori activity and settlement, as it is both an indicator of landscape disturbance (i.e., it is one of the first post-fire successional species) and a nutritional resource (McGlone and Wilmshurst 1999; McWethy et al., 2010; Newnham et al., 2018). The period prior to the marked increase in bracken fern is called the pre-human phase, and the period following is referred to as evidence of Māori settlement, hereafter Māori settlement. Pine (*Pinus* spp.) and other non-native plants including willow (*Salix* spp.), sheep sorrel (*Rumex acetosella*) and Alder (*Alnus* spp.) were introduced by European colonialists and are used to mark the start of European activity; this period is referred to as post-European.

2.4. Geochemical analysis

The relative abundance of trace elements was measured down the cores using a Cox Analytics Itrax Core Scanner at the University of Otago Repository for Core Analysis. The core was scanned using a molybdenum X-ray tube configured at 30 kv, 55 ma and 10 s integration time. Changes in the ratio of manganese to iron (Mn:Fe; Davison 1993) was used as proxy for past lake redox conditions and the ratio of titanium to incoherent scattering (Ti:inc) to infer shifts in terrigenous influx (Davies et al., 2015).

Cadmium was used as a proxy for agricultural superphosphate fertilizer application in the landscape around the lakes (Gray and Cavanagh 2023). Sediment core sub-samples (15 for Lake Alice and 23 for Lake Wiritoa) were selected to ensure there were some baseline samples in the prehuman and Māori settlement phases. We then focused on selecting sub-samples from depths which corresponded to about CE 1950 which is when we anticipated superphosphate fertilizer application increased. The subsamples were dried, passed through a 2 mm sieve and analysed for cadmium using acid digestion followed by ICP-MS, based on the US EPA method 200.8 with a reporting limit of 12.5 mg kg^{-1} . A mass accumulation rate was determined using the age models, and these data were used to convert the concentrations into a flux to account for changes in sedimentation rates and density through time.

2.5. Temperature data

Landscape annual mean temperatures and annual mean temperatures anomalies (difference from 1961 to 1990 normal; NIWA 2017) data were obtained from the National Institute of Water and Atmospheric climate database (cliflo.niwa.co.nz) from the Palmerston North metrological station ($40^{\circ}38'2''\text{S}$, $175^{\circ}60'09''\text{E}$). Data was available from 1931 to 2022.

Historical mean temperature data (850–1999 CE) was obtained from the GISS-E2-R (Rind et al., 2020) global model utilising the grid outputs encompassing Aotearoa-New Zealand. Grid cells from the Southwest North Island climate region were selected based on the climate regions of Kidson (Kidson 2000). This model was chosen after an evaluation including five other climate models (CSIRO-Mk3L-1-2 (Phipps et al., 2012), MIROC-ES2L (Ohgaito et al., 2021), MPI-ESM-P (Gutjahr et al., 2019), MRI-CGCM3 (Yukimoto et al., 2012) and MRI-ESM2-0

(Yukimoto et al., 2019) because it showed the closest alignment to the Palmerston North metrological station measured data between the overlapping periods of 1931 to 1999. Annual mean temperatures anomalies were calculated as the difference from the 1961–1990 mean for both the modelled and measured data. The data was normalised to 0 by calculating the mean for the entire period of the modelled climate model (850–1999) and removing this value from the 1961–1990 mean. Data were plotted as 15 year running means.

2.6. DNA extraction, droplet digital PCR and metabarcoding

DNA extraction, polymerase chain reaction (PCR) and droplet digital PCR (ddPCR) set-up, template addition and PCR/ddPCR analysis steps were conducted in dedicated laboratories equipped with ultraviolet sterilization that was activated for at least 15 mins before and after each use. The PCR/ddPCR set-up and template addition were conducted within laminar flow cabinets equipped with HEPA filtration. Throughout the process, we used aerosol barrier tips (Axygen, USA) for PCR or epT.I.P.S. (Eppendorf, Germany) for ddPCR.

Sub-samples (~0.25 g; $n = 35$ Lake Alice, and $n = 44$ Lake Wiritoa) of sediment were weighed and DNA extracted using the DNeasy PowerSoil™ DNA Isolation Kit (QIAGEN, Germany) following the manufacturer's protocol. DNA extraction was performed in batches of ten to twelve samples, including a negative control for every two batches containing all reagents but no sediment. DNA concentrations and quality were measured using a Spectrophotometer (Eppendorf).

The general bacterial community was characterised as a proxy for changes in water quality using amplicon sequencing. The V3–V4 region of the 16S ribosomal rRNA (16S rRNA) gene was amplified by polymerase chain reaction (PCR) using bacterial specific primers 341F: 5'-CCT ACG GGN GGC WGC AG-3' and 805R: 5'-GAC TAC HVG GGT ATC TAA TCC-3' (Klindworth et al., 2013). DNA extraction and PCRs were conducted as described in Pearman et al. (2020). Library preparation was undertaken following the Illumina 16S metagenomics library prep manual and sequencing undertaken on an Illumina MiSeq™ at Auckland University (Aotearoa New Zealand). Bioinformatics, and quality control were conducted as described in Pearman et al. (2020).

Microbial metabolic community functions were inferred using the PAPRICA bioinformatic pipeline (Bowman and Ducklow 2015). Sequences for each amplicon sequence variant (ASV) were created by re-replicating the sequences to match their abundance within a sample. Sequences were phylogenetically placed into a reference phylogenetic tree containing the 16S rRNA gene of sequenced genomes. Each node of the tree had a consensus genome and functional inference was determined for a query sequence based on the nearest node. Functional inference used the MetaCyc database (Caspi et al., 2007), and we focussed on the dissimilatory nitrate reduction to ammonia (DNRA) bacterial functional data.

Droplet digital Polymerase Chain Reaction (ddPCR) was used to quantify the copy numbers of cyanobacterial 16S rRNA genes in each sample using the CYAN 108F and CYAN 377R primers targeting an approximate 270 base-pairs (bp) region (Picard et al. (2022a)). At least one negative methodological control (RNA/DNA-free water; Life Technologies), and a positive biological control (DNA extracted from a cyanobacterial culture) were included. Droplet digital PCR copy numbers (copies/ng) were normalised by total DNA concentration ($\text{ng } \mu\text{L}^{-1}$).

To further characterise the cyanobacterial composition cyanobacterial-specific metabarcoding was undertaken. PCRs were performed using the cyanobacteria-specific primers CYB359-F and CYB784-R (Nübel et al., 1997) to amplify an approximately 400 bp fragment of the V3-V4 regions of the 16S rRNA gene. Negative extraction and PCR controls were included. PCRs and bioinformatics were undertaken as described in Picard et al. (2022a) with the exception that the SILVA database was used for taxonomic assignment and this was adapted with the updated cyanobacterial classifications from CyanoSeq (Lefler et al., 2023). The sequence FASTA files from the bacterial and

cyanobacterial metabarcoding have been deposited in the Short Read Archive under PRJNA10006432 and PRJNA1006146 respectively.

2.7. Hyperspectral scanning

The cores were scanned using a Hyperspectral Core Scanner equipped with a Specim sCMOS-CL-50-V10E-SCB camera working in the visible to near-infrared range (400–1000 nm). Measurements were captured with a spectral resolution of 1.3 nm and a spatial resolution of 41 μm . This study analysed spectral data using RABD₆₆₀₋₆₇₀, an index which is correlated with the sedimentary pigment chlorophyll-a and its degradation products (Butz et al., 2017; Schneider et al., 2018). The index was then converted to a Chl-a proxy ($\mu\text{g/g}$) using a conversion factor determined through a comparison of lake surface samples from 94 lakes in Aotearoa New Zealand where Chl-a was measured using both high performance liquid chromatography and the hyperspectral scanning (Yackulic, Shepherd, Puddick and McKay, unpublished data). The Chl-a data was converted to flux ($\mu\text{g cm}^{-2} \text{ yr}^{-1}$) following the methods used for cadmium.

2.8. Statistical analyses

The composition of the bacterial data was clustered in the R package vegan (Oksanen et al., 2007) using the Bray-Curtis method and constrained stratigraphically using the chclust function (method = CONISS) within the package rioja (Juggins 2019). A dendrogram of the results was plotted in ggplot2 (Wickham 2016). Principal response curves (PRC) were constructed for the bacterial data based on the Hellinger transformed bacterial community data within the package analogue (method "ca", maxit = 50; Simpson et al., 2021). The community composition of both the bacteria and cyanobacteria communities were plotted against date as relative abundance bar plots in the package ggplot2. A generalized linear model (GLM) was undertaken in the stats package in R to examine the effect of DNRA (as a proxy for nutrients), temperature anomalies, Mn:Fe (as a proxy for redox conditions), and Ti:Inc (as a proxy for erosion) on cyanobacterial abundance (ddPCR).

3. Results

3.1. Recorded human and environmental history

Archaeological evidence, including the presence of shellfish pits, settlements, and middens, suggests that before 1400 CE, Māori lived a semi-nomadic lifestyle in this region, later transitioning to larger tribal settlements (Marr 2003). While the exact timing of European arrival in the Manawātū-Whanganui area is uncertain, it is likely to have occurred around the 1830s CE (Marr 2003). Early settler accounts reflect centuries of Māori activity in the region, including forest clearance and subsequent growth of indigenous scrub, grasses, rushes, and flax (Hocking 1964; Marr 2003). The post-European arrival landscape transformation appears to have been swift, with the catchments of both lakes quickly converted to agricultural use. The earliest written account of Lake Alice is from 1858, describing the land as sheep farmland planted with English grass (Hickson 1858). Dairy farming was first recorded around Lake Alice in 1913 (Rangitikei County Council 1907). Dairy farms were established near Lake Wiritoa in 1841, and journal entries and letters from 1843 describe the land as having been cleared and a dairy herd present (McPhail 2015). By 1858, the area between Lake Wiritoa and the Whanganui River was a mixture of pasture, horticulture, bush and bracken fern (Lees 1858). The first areal application of high phosphate artificial fertilizer in this region was reported in 1950 (Wanganui Chronicle 1950).

The encroachment of sand dunes onto pasture was identified as a key concern for settlers in the early 1900s in this region. Experimental planting of exotic pine to stabilize the landscape started in 1916, with *Pinus radiata* the preferred species (McKelvey 1999). The exact planting

dates around Lakes Alice and Wiritoa are unknown, although the largest forest in close proximity to the lakes today was in its second rotation in 1988, indicating that the forest was likely originally planted between 1950 and 1965 (McKelvey 1999; Ellegard 2019).

The Lake Alice Hospital was the most significant urban development close (1 km away) to Lake Alice, and water was temporarily drawn from the lake for the facility in 1948 when the water tower commenced operation (Wanganui Chronicle 1948). The hospital was closed in 1999, and the land reverted to dairy farming. Development around Lake Wiritoa increased after the 1940s with construction of a campground in 1951 and recreational facilities, including water skiing facilities during the 1970s (NZ Press Association 1971). Wanganui Prison was constructed in 1978 on the south bank of the hydrologically connected Lake Pauri (Fig. 1; Department of Corrections 2010; Gibbs and Champion 2013). While the prison's sewage treatment plant discharged treated effluent to land at the south of the facility, stormwater is discharged directly into Lake Pauri near its ephemeral connection to Lake Wiritoa (Gibbs and Champion 2013).

The exact dates of the introduction of non-native fish to Lake Alice are unknown, but they are very likely similar to Lake Wiritoa. Lake Wiritoa was a primary location for the introduction of exotic species by the Whanganui Acclimatisation Society. Black swans (*Cygnus atratus*) were released in 1866 and formed a breeding population (Nelson Examiner 1867). Carp (*Cyprinidae*), perch (*Perca fluviatilis*) and trout (*Salmonidae*) were released into the lake in 1868 (Wanganui Herald 1868a, 1868b). Tench (*Tinca tinca*) and more perch were ordered from Melbourne in November 1870 for release (Wanganui Herald 1870). These species have been detected in the lake from the 1970s to the present.

3.2. External stressors – vegetation, terrigenous influx, cadmium flux and temperature

The Lake Alice sediment core covers a period dating to about 1622 CE (1546–1705 CE; HDPF 95 % range), with no sediment representing the pre-human era recovered (Supplementary Fig. 1). The pollen spectra are characterised by high relative abundances of bracken fern and tutu or tāweku (*Coriaria arborea*) indicating significant vegetation change had already occurred (Fig. 2; Supplementary Fig. 2). Relatively low amounts of native tall tree pollen are present compared to what would be expected in the pre-human period, suggesting the persistence of small stands of podocarps including kahikatea (*Dacrycarpus dacrydioides*),

mataī (*Prumnopitys taxifolia*) and tawhai raunui (southern beech; *Fuscopora*) in the region (Supplementary Fig. 2). After 1862 CE (1848–1877 CE), an increased prevalence of grasses (Poaceae) and the emergence and increase in abundance of pine (*Pinus*) in the pollen record, closely coincides with the near-complete decline of small native trees and shrubs as well as bracken fern and tutu (Fig. 2). These changes in the pollen profile delineate the shift from Māori land use practices to the establishment of agriculture and later commercial forestry.

The Lake Wiritoa sediment core extends to before human arrival, with the lowest layers dated to around 798 CE (667–907 CE; Supplementary Fig. 3). Tall trees including kahikatea, mataī, and tawhai raunui dominate the pollen sum (Fig. 2; Supplementary Fig. 4). The abundance of tall native tree pollen declined rapidly after about 1394 CE (1312–1485 CE) coinciding with a rapid increase in bracken fern and tutu pollen and charcoal concentrations consistent with Māori settlement in the region. Post about 1858 CE (1844–1870 CE) the pollen follows the profiles observed in Lake Alice with pine appearing and increasing in abundance and a dramatic increase in grasses and a decline in bracken fern and tutu pollen and charcoal (Fig. 2).

Terrigenous influx (Ti:Inc) to both lakes was variable, with a marked increase occurring in Lake Alice between 1877 CE (1863–1891 CE) and 1993 CE (1989–1996 CE; Fig. 3). Conversely, historic terrigenous influx rates were quite high in Lake Wiritoa and decreased notably about 1394 (1312–1485 CE), before increasing again briefly around 1839 (1806–1869 CE) and then decreasing to the uppermost portion of the sediment core (Fig. 3). Cadmium flux remained consistently low in both lakes until around 1950 CE, after which there is an abrupt increase with elevated levels remaining until the top of the sediment core (Fig. 3). The proxy for redox conditions (Mn:Fe) is variable but relatively low in both lakes, except for a large peak in Lake Wiritoa starting in 2011 CE (2010 to CE 2017).

Analysis of the measured annual mean temperature anomalies showed a significant increase of about 1.1°C ($p < 0.001$) between 1931 and 2022 (Fig. 4A). The long-term data showed marked variability in mean annual temperature anomalies, with a notable decrease about 1600 CE (Fig. 4B).

3.3. Biological response variables

Distinct bacterial communities were identified in Lake Alice pre and post 1910 CE (1901 to 1919 CE; Fig. 5). In Wiritoa, four distinct communities align with the periods of human occupation and a post 1983 CE

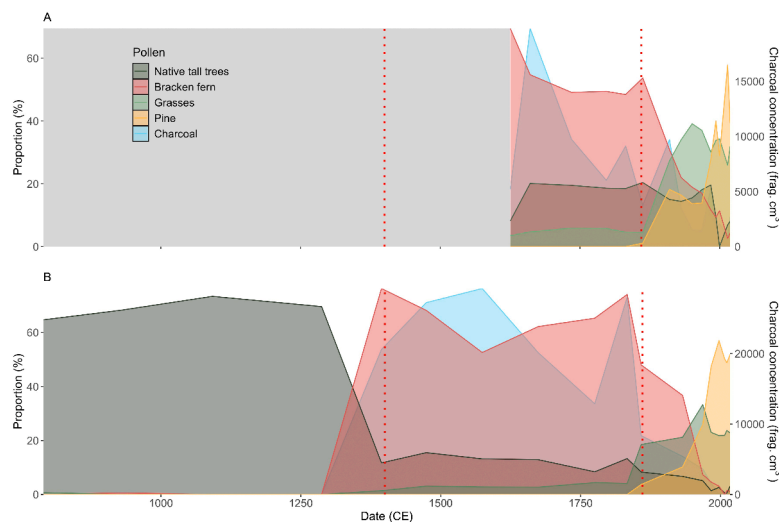


Fig. 2. Percent dryland taxa of selected pollen taxa sum of tall native trees, bracken fern (*Pteridium esculentum*), grasses (Poaceae), and pine (*Pinus*) and macro-charcoal concentrations for; (A) Alice and (B) Wiritoa. The light grey box in (A) represents no data. Dashed red vertical lines show occupation periods; pre-human left of first line, Māori settlement between lines, and post European settlement to far right of lines.

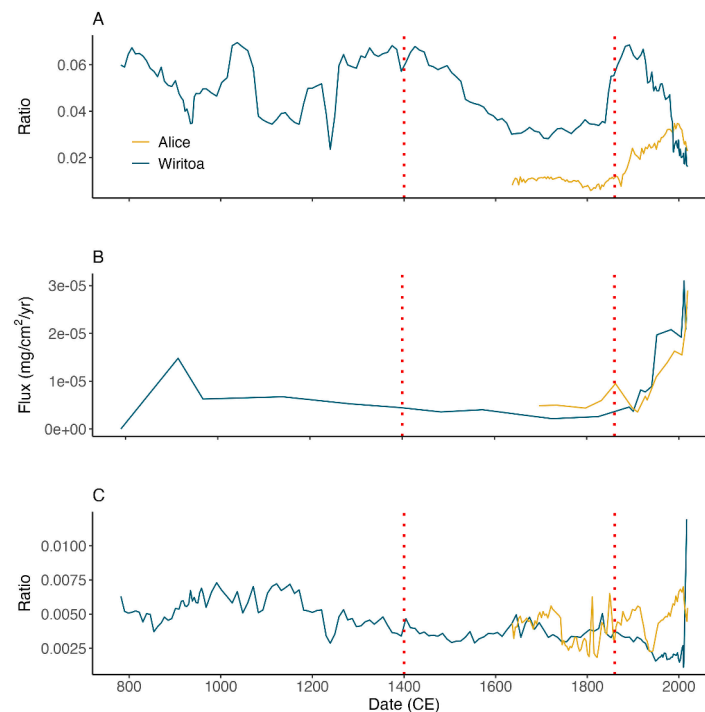


Fig. 3. Summary of geochemical data. (A) Terrigenous influx (titanium to incoherent scattering, Ti:Inc), (B) Cadmium flux, and (C) redox conditions proxy (manganese:iron (Mn:Fe) ratio). Dashed vertical lines show occupation periods; prehuman left of first line, Māori settlement between lines, and post European settlement to far right of lines.

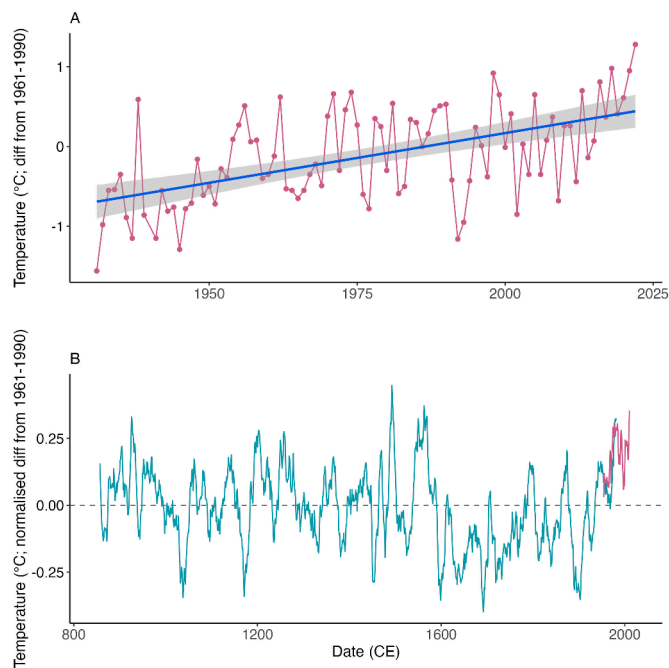


Fig. 4. (A) Temperature departures from the 1961–1990 normal for the Palmerston North meteorological station (40°38'2"S, 175°60'09"E). (B) Modelled (GISS-E2-R; 850 to 1999 CE; blue) and measured (1931–2022; pink; Palmerston North meteorological station) temperature departures from the 1961–1990 normal plotted as a 30-year moving average.

(1975 to 1988 CE) shift, with the most pronounced change occurring between the Māori settlement and post-European periods (Fig. 5). The most notable changes in both lakes involve decrease in Dehalococcoidia and an increase Gammaproteobacteria, Verrucomicrobiae and Thermodesulfobivibrionia during the post-European period.

The PRC showed a gradual shift in bacterial community in Lake Alice until 1951 CE (1943 to 1957 CE) when there was a distinct change that coincided with an increase in the dissimilatory nitrate reduction bacterial functional profile (Fig. 6). In Lake Wiritoa there was a gradual shift in bacterial community composition until 1858 CE (1844 to 1870 CE), when it changed markedly concomitant with an increase in the dissimilatory nitrate reduction functional profile (Fig. 6).

The hyperspectral derived chl-a flux was relatively stable in both lakes until about 1930 CE when it increased slightly in Lake Alice before plateauing until rising again markedly in about 2005 CE (Fig. 6). The increase began slightly later in Lake Wiritoa (~1940) with a steady increase until current day. The cyanobacterial 16S rRNA copy numbers were low and stable in Lake Alice until about 1943 CE (1936 – 1950 CE) when they increased above background levels and continued rising to the sediment core surface (Fig. 6D). A similar pattern was observed in Lake Wiritoa, but the increase began a little later (1974 – 1987 CE; Fig. 6D).

The metabarcoding data shows low levels of cyanobacteria in the prehuman and Māori settlement periods, which are dominated by the picocyanobacteria *Cyanobium* (Fig. 7A & B). Bloom forming genera (i.e., *Dolichospermum*, *Microcystis*) were first detected in Lake Alice in 1854 CE (1839–1870 CE), but their abundance increases notably in 1984 CE (1982–1985 CE; Fig. 7A). *Dolichospermum* was the predominant genus peaking at 25 % in 2012, however *Microcystis* increased in abundance after 2014 CE (2012–2015 CE). In contrast bloom forming genera were not detected in Lake Wiritoa until 1970 CE (1963–1975 CE) and become more abundant from 1997 CE (1990–2007 CE) when *Dolichospermum* was present, with *Microcystis* the most prominent genera after 2007 (2006–2009 CE) reaching 38 % of the community in 2017 (Fig. 7B).

A GLM was used to investigate the contribution of nutrients (DNRA), temperature (temperature anomalies), redox conditions (Mn:Fe), and erosion (Ti:Inc) in driving the abundance of cyanobacteria (ddPCR). In Lake Alice nutrients ($p = 0.03$) and erosion ($p = 0.007$) had a statistically significant effect, while in Lake Wiritoa nutrients ($p = 0.01$) and redox conditions ($p = 0.006$) were significant.

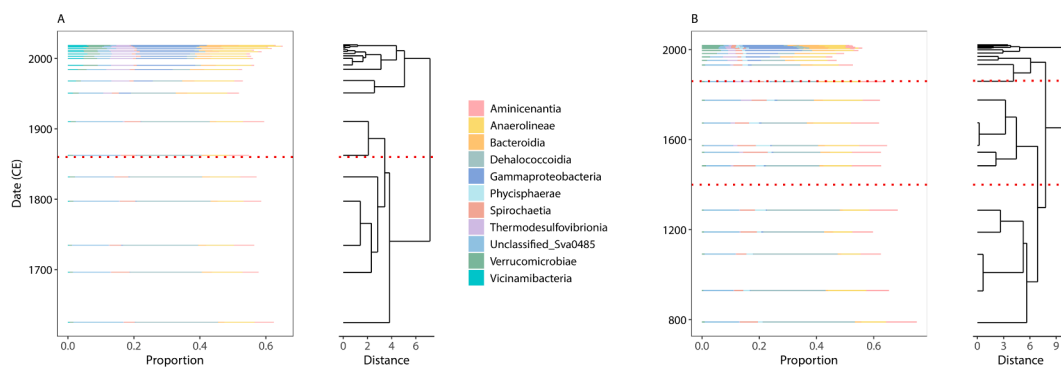


Fig. 5. Bacterial sedimentary ancient DNA amplicon species variants presented as relative abundance at the class level (A) Lake Alice, (B) Lake Wiritoa. Only the top 10 taxonomic classes per lake were plotted. CONISS plots are shown to right of abundance graphs. Note y-axis scale varies.

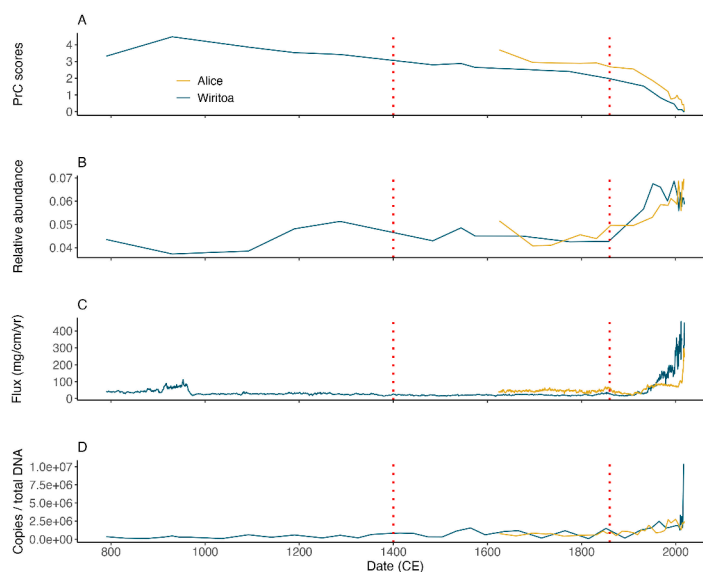


Fig. 6. Summary of biological data. (A) Principal response curve (PRC) for sedimentary ancient DNA (sedaDNA) bacterial community composition, (B) bacterial dissimilatory nitrate reduction to ammonia functional profile from sedaDNA, (C) chlorophyll-*a* flux ($\text{mg cm}^{-1} \text{yr}^{-1}$), and (D) droplet digital PCR data for the 16S ribosomal RNA cyanobacterial data. Dashed vertical lines show occupation periods; prehuman left of first line, Māori settlement between lines, and post European settlement to far right of lines.

4. Discussion

The drivers of cyanobacterial bloom initiation and subsequent intensification can be complex and varied (Carey et al., 2012; Jankowiak et al., 2019). A suite of techniques including real time monitoring, modelling, and satellite imagery have been applied to better understand the occurrence of cyanobacterial blooms and to measure or predict the role various stressors (e.g., nutrient inputs, non-native species, warming water temperatures) play in driving their formation (Zamyadi et al., 2016; Rouso et al., 2020; Coffey et al., 2021). In general, these methods are applied to lakes with existing blooms, and because of the short duration of most monitoring records studies exploring the onset of cyanobacterial blooms are limited.

We reconstructed long-term records of cyanobacterial abundance, external stressors and internal lake processes using sedaDNA and paleolimnological techniques informed by historical information. Using this approach, we determined the timing of the arrival of bloom-forming species and their subsequent increase in abundance in two lakes with contrasting areas and depths but similar land use regimes. This allowed us to investigate the dynamics of cyanobacteria as they establish, and to explore how different human-mediated stressors contribute to bloom formation.

The base of the sediment core from Lake Wiritoa predates human

arrival in Aotearoa New Zealand, allowing for the assessment of changes across a full spectrum of anthropogenic effects, from subsistence practices to the initial European impact and subsequent intensification. In contrast, the Lake Alice core begins approximately 200–300 years after the estimated arrival of Māori in this region. In the following discussion, we initially examine the timing of the emergence of bloom-forming cyanobacteria and the increase in their abundance in the two study lakes. We then explore the various stressors and associated ecosystem and cyanobacterial responses.

4.1. Increases in abundances of bloom forming cyanobacteria

In the pre-human and Māori phases the cyanobacterial community was dominated by picocyanobacteria, primarily *Cyanobium*. This result concurs with previous studies of historical cyanobacterial communities in Aotearoa New Zealand (Picard et al., 2022a) and this finding, in concert with the other data in this study, indicates that nutrient levels were lower and there was higher water clarity over these periods. Recent research indicates that picocyanobacteria DNA may degrade slower than other bloom forming cyanobacteria (Mejbel et al., 2022). While this is unlikely to explain the shift observed in this study it highlights the need to take caution when interpreting DNA based results.

Of note was the complete absence of common bloom forming genera

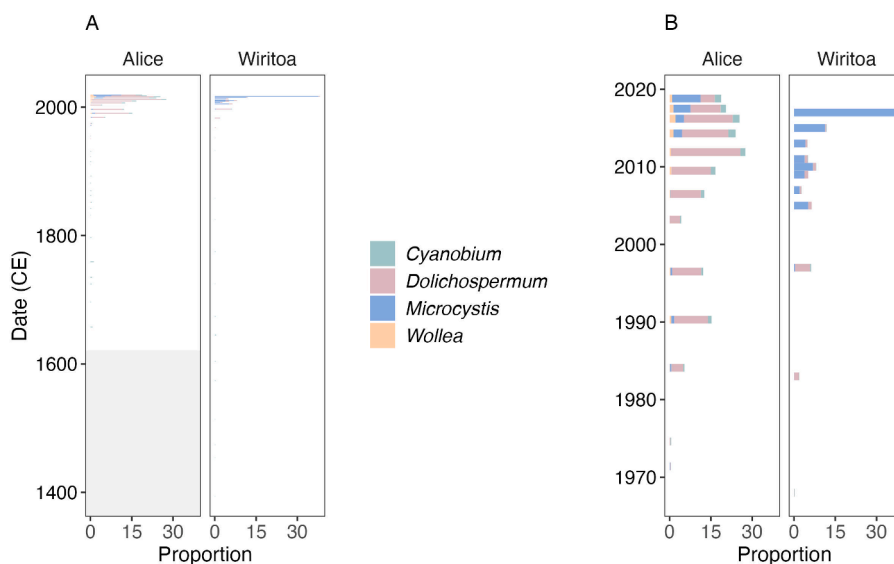


Fig. 7. Cyanobacterial sedimentary ancient DNA amplicon species variants presented as relative abundance at the genera level (A). The last 50 years of the sediment core (B). Only species with $\geq 0.05\%$ abundance are shown. Light grey box in (A) shows area with no data.

in these lakes during the pre-human and Māori phases. These genera may have been present in the lakes at very low levels. Alternatively, they could have been accidentally introduced. The timing in Lake Alice corresponds approximately to when non-native fish were introduced (~1868 CE). While conclusive evidence to support this hypothesis is lacking, studies have shown an association between freshwater non-native fish and zooplankton ‘hitchhikers’ in Aotearoa New Zealand (Duggan and Pullan 2017). Birds, such as black swans, which were introduced to this region of Aotearoa Zealand around 1860 CE could also have been another vector. Bloom-forming genera were recorded about 85 years earlier in Lake Alice than Lake Wiritoa, albeit the levels were initially very low in Lake Alice. It is plausible that the molecular signal from these genera is diluted in the larger deeper Lake Wiritoa, and they were not detected until they become well established.

The molecular data indicates the increase in abundance of key bloom-forming species begins in Lake Alice about 15 years before Lake Wiritoa. Modelled data indicates Lake Alice’s decline in water quality may have been exacerbated by a much higher areal nutrient load than Lake Wiritoa (see Methods Section). Shallow lakes are more vulnerable to damage from human activities and environmental changes in their catchments (including nutrient pollution and temperature warming) because of their large surface-to-volume ratio (Feuchtmayr et al., 2009). The shallow nature of Lake Alice, may have therefore led to higher nutrient loads and warmer water temperatures, potentially facilitating the earlier onset of increases in cyanobacterial abundance (Lürding et al., 2018), however data to confirm this is lacking. Carp (present in both lakes) have also been shown to facilitate shifts in water clarity in shallow lakes due to their benthic foraging physically uprooting aquatic vegetation, causing sediment suspension and mobilising nutrients into the water column (Weber and Brown 2009). Although it is likely the timing of carp release into the lakes was similar, their impact may have been greater in Lake Alice due to its shallow depth.

Despite *Dolichospermum* and *Microcystis* being present in both lakes, *Dolichospermum* initially dominates in Lake Alice while *Microcystis* is most abundant in Lake Wiritoa. *Dolichospermum* is diazotrophic and can fix atmospheric nitrogen into biologically available nitrate in order to satisfy their nitrogen requirements for growth (Schindler et al., 2008). Diazotrophic cyanobacteria are usually dominant when the total nitrogen to total phosphorus (TN/TP) ratio is low, or when nitrogen is limiting (Reynolds 2006). In contrast, non-diazotrophic cyanobacteria, such as *Microcystis*, require a biologically available nitrogen source and generally dominate when it is in excess, however this paradigm does not

always hold true (Xu et al., 2010). Temperature has also been shown to drive the relative dominance of *Dolichospermum* and *Microcystis*, although results from different water bodies are confounding (Rigosi et al., 2014). The deeper water column of Lake Wiritoa may also favour *Microcystis* which is very effective at regulating its buoyancy allowing it to access nutrient rich water in the hypolimnion during stratification (Li et al., 2016). While we cannot delineate the historical drivers of variations in cyanobacterial genera between Lakes Alice and Wiritoa, the existence of these differences implies that human impacts on the landscape and lakes had diverse effects on the progressive eutrophication of these water bodies.

The increase in magnitude of the total cyanobacteria is similar among the two lakes except for very high concentrations recorded in the uppermost samples from Lake Wiritoa. This aligns with a peak in the Mn:Fe ratio, a proxy for redox conditions. Hypoxia in a stratified water column can result in the release of phosphorus from the sediments (Wang et al., 2016), which may be fuelling prolific cyanobacteria growth in this lake (Smucker et al., 2021).

The changes in hyperspectral derived chl-*a* did not follow the changes observed using the cyanobacterial ddPCR with the chl-*a* flux increasing earlier in both lakes. This is not surprising given that most algae contain chl-*a*. These earlier shifts in chl-*a* likely represent changes in other non-cyanobacterial genera such as diatoms and provides another avenue to detect the early onset of eutrophication (Gregersen et al., 2022). This highlights the benefits of using complementary methods to explore shifts in primary producers in lakes.

4.2. External stressors and their relationship with the onset and proliferation of cyanobacterial blooms

Changes in vegetation around Lakes Alice and Wiritoa conform to other studies in Aotearoa New Zealand, which have shown rapid fire-mediated forest reduction by Māori, transforming extensive areas into scrubland. The further widespread clearance of forests by European settlers resulted in additional disturbance of previously fire-affected soils, amplifying sediment inputs into Lakes Alice and Wiritoa, as evidenced by the increase in Ti:inc ratio in both sediment cores. Early signs of an ecosystem response to human impacts are observed in shifts in bacterial composition in Lake Wiritoa, concurrent with the decline in native forest. However, the dissimilatory nitrate reduction bacterial functional profile, and cyanobacteria abundance and community composition, exhibited relative stability during the Māori settlement,

suggesting that lake water quality remained high.

The second significant change in the bacterial community composition in Lake Wiritoa, and the first in Lake Alice change coincides with an increase in terrigenous influx in both lakes and, the onset of pollen markers associated with European activity in the catchment. In both lakes this structural shift also aligns with an increase in the dissimilatory nitrate reduction bacterial functional profile, likely signalling the start of a progression towards eutrophication.

These lakes were some of the first in the country where non-native fish such as perch and carp were introduced, and the overlap in their introduction and the shift to post-European agricultural land use makes it very hard to delineate the relative importance of these drivers. Both lakes show a further shift in bacterial community composition in approximately 1950 CE which overlaps with the onset of increases in fertiliser (indicated by the cadmium proxy) and historical records of aerial top-dressing commencement in the region. Commercial pine forestry and associated nitrogen fertilizer use also began in the wider region in the 1950 to 1960's potentially adding a further stressor to already perturbed lakes.

There was a lag time between these additions of nutrients to the landscape and the onset of increases in cyanobacterial abundance, and as noted above this was longer in Lake Wiritoa than Lake Alice. The pollen data (Supplementary Figs. 2 and 4) indicates that both lakes had substantial wetlands containing *Typha* and Cyperaceae, and macrophytes including *Myriophyllum* and *Potamogeton*, that might have initially buffered and utilised these increased nutrient inputs. Increasing nutrient inputs as evident from the rising cadmium fluxes and increasing bacteria dissimilatory nitrate reduction bacterial functional profile, suggest that ultimately excess nutrients decreased the water quality to a point optimal for bloom-forming cyanobacteria to thrive.

The GLM analysis indicates that nutrients, or parameters related to nutrients (i.e., erosion which brings nutrients into lakes, or low oxygen levels can cause the release of nutrients stored in the sediment), were the main drivers of increases in cyanobacterial abundance in both lakes. In contrast temperature was not significant. In the Manawatū-Whanganui region, temperatures have increased by about 1.1 °C between 1929 and 2022 CE. Globally climate change is emerging as a significant factor influencing the occurrence and intensity of cyanobacteria blooms. Rising temperatures and altered precipitation patterns can lead to increased water temperatures and changes in nutrient availability, creating favourable conditions for the growth of cyanobacteria (O'Neil et al., 2012). Although it seems unlikely that increases in temperature were a key driver in initiating the blooms in the study lakes, it will likely intensify them in the future.

5. Conclusions

We documented increases in cyanobacterial abundance and a shift to dominance of bloom-forming genera in two lakes of different size and depth. Despite both lakes experiencing similar stressors, cyanobacteria increased in abundance above pre-European background levels sooner in the smaller, shallower Lake Alice. This is most likely because shallow lakes are more vulnerable to nutrient pollution and environmental changes, due to their large surface-to-volume ratio. The data indicates that cyanobacterial abundance is now higher in the deeper, larger Lake Wiritoa, likely due to hypoxia and the release of phosphorus from the sediments. The most likely cause of the cyanobacterial blooms is a result of excess nutrients, a pattern that is consistent with global trends (Erratt et al., 2023b). However, the synchronous timing of increasing nutrients and the introduction of non-native species means it is not possible to fully delineate the relative importance these stressors played in driving bloom formation in these lakes.

CRedit authorship contribution statement

Caitlin Wheeler: Conceptualization, Data curation, Formal analysis,

Investigation, Methodology, Writing – original draft, Writing – review & editing. **John K. Pearman:** Data curation, Formal analysis, Methodology, Software, Writing – original draft, Writing – review & editing. **Jamie D. Howarth:** Data curation, Formal analysis, Methodology, Validation, Visualization, Writing – review & editing. **Marcus J. Vanderdoes:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Katherine Holt:** Conceptualization, Investigation, Supervision, Writing – review & editing. **Steven A. Treweek:** Conceptualization, Formal analysis, Methodology, Supervision, Writing – original draft, Writing – review & editing. **Xun Li:** Data curation, Formal analysis, Validation, Writing – review & editing. **Lucy Thompson:** Data curation, Formal analysis, Validation, Writing – review & editing. **Georgia Thomson-Laing:** Data curation, Formal analysis, Validation, Visualization, Writing – review & editing. **Mails Picard:** Data curation, Formal analysis, Writing – review & editing. **Chris Moy:** Data curation, Formal analysis, Validation, Writing – review & editing. **Nicholas P. Mckay:** Data curation, Formal analysis, Visualization, Writing – review & editing. **Adelaine Moody:** Data curation, Formal analysis, Writing – review & editing. **Claire Shepherd:** Data curation, Formal analysis, Writing – review & editing. **Valerie van den Bos:** Data curation, Formal analysis, Writing – review & editing. **Konstanze Steiner:** Data curation, Formal analysis, Writing – review & editing. **Susanna A Wood:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.hal.2023.102563](https://doi.org/10.1016/j.hal.2023.102563).

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