Cyanobacteria species dominance and diversity in three Australian drinking water reservoirs

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Abstract The objective of this study was to identify correlations between environmental variables and cyanobacterial diversity, succession and dominance in three Australian water supply reservoirs. We assessed up to 15 years of in-lake water quality monitoring data from Lake Wivenhoe and Lake Tingalpa (Queensland), and Lake Myponga (South Australia). Lakes Wivenhoe and Tingalpa, subject to a subtropical climate, had higher cyanobacterial richness than Lake Myponga in temperate South Australia. Richness in the subtropical lakes was positively correlated ($P < 0.05$) with total cyanobacteria biomass, and cyanobacteria biovolume $> 0.03 \text{ mm}^3/\text{l}$ (Alert level 1; World Health Organization) was often composed of multiple cyanobacteria species. Peaks in

total cyanobacteria biomass and diversity occurred in all three lakes from late spring to early autumn. Unicellular picocyanobacterial dominance was negatively correlated ($P < 0.05$) with total nitrogen while dominance of colonial and filamentous species with larger cells (e.g. *Microcystis* spp., *Raphidiopsis* spp., *Dolichospermum circinale*) was positively correlated ($P < 0.05$) with total phosphorus. Among the species with larger cells, diazotrophic *D. circinale* often dominated when total nitrogen was at low concentrations. Our results support decision making for selecting cyanoHAB control strategies based on single- or multi-species dominance and reinforce that new monitoring technologies could support species-level assessments.

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Introduction

Phytoplankton regulate many ecological processes in waterbodies, and understanding their dynamics is, therefore, essential to optimize water resources management and support aquatic ecosystem health (Willén, 2000). Eutrophication modifies phytoplankton community structure, which can potentially lead to harmful algal blooms, often dominated by cyanobacteria (cyanoHABs). CyanoHABs impact the ecology and economics of water resources, and human health, especially when associated with production of cyanotoxins (Metcalf & Codd, 2012) and taste and odour compounds (Watson et al., 2016). Their ecological impacts include changes in community structure, trophic cascades and biogeochemical cycles of waterbodies (Sukenic et al., 2015).

Cyanobacteria are ancient microorganisms adapted to a wide range of environmental conditions. Variations in cyanobacteria morphology (e.g. cell size and colony formation, Whitton & Potts, 2007; Xiao et al., 2018), gas vesicles for floatation (Pfeifer, 2012), metabolic processes (e.g. diazotrophy, Bryant, 2006) and toxin production (Catherine et al., 2013) support adaptation to a wide range of habitats and are associated with the cosmopolitan distribution of cyanobacteria. Species-specific traits interact in complex ways with environmental conditions that influence the timing and magnitude of cyanoHABs. Understanding cyanobacterial succession and dominance can improve water resources management by controlling environmental drivers that may otherwise stimulate cyanoHABs species (Dokulil & Teubner, 2000). Current scientific understanding of cyanoHABs derives mostly from field observations of cyanobacteria succession or laboratory experiments focused on their physiology.

Laboratory experiments have been used to isolate the factors that affect cyanobacteria growth, but they do not simulate synergistic or antagonistic responses to multiple variables that cannot be replicated *in vitro* (Reynolds & Irish, 1997). Field studies of changes in abundance or biomass of species through time at a particular location are commonly used to understand cyanobacteria community adaptation to changes in environmental conditions and to test hypotheses related to cyanobacteria ecology (Ludwig et al., 1988).

Shifts to cyanobacterial dominance in phytoplankton communities, commonly associated with

cyanoHABs, have been observed in lakes in different climatic zones and regions of the world (see (Niamien-Ebrotte et al., 2015)). Increases in eutrophication and temperature are widely accepted as favouring cyanobacteria dominance over other phytoplankton groups (Dokulil & Teubner, 2000). However, the high diversity of cyanobacteria and the wide variety of adaptive traits among species, strains and ecotypes (Mur et al., 1993; Ye et al. 2019) result in many other abiotic factors contributing to shifts in cyanobacterial species dominance. For instance, thermal stratification and mixing patterns (Paerl & Huisman, 2009), water transparency (Vanderley et al., 2021), nitrogen to phosphorus ratios (Zhang & Rao, 2012), chemical oxidation state of inorganic nutrients (Amorim et al., 2020; Zhang et al., 2021), wind (Liu et al., 2019) and water level (Brasil et al., 2016) have been linked to dominance of particular cyanobacteria species. Idealistic generalizations of species-specific environmental drivers are complicated by site-specific factors that characterize most studies and limit broader interpretations about interactions among species (Dokulil & Teubner, 2000). This limitation points to the need for studies that synthesize relationships of cyanobacterial dominance with environmental conditions and habitats (see Rousso et al., 2020) and link trophic level and climatic region.

Dominance metrics are commonly used to characterize and quantify the dominant species in a community (McNaughton, 1967). Cyanobacteria species dominance can be quantified by peaks in numbers of individuals (cell counts) (Fernández et al., 2015), relative abundance of cells (Zhang et al., 2021) and biomass (biovolume) (Amorim et al., 2020; Yang et al., 2016). The choice of cell counts or biomass may yield different interpretations of dominance because of the wide range of sizes of cyanobacteria cells (Hillebrand et al., 1999). Cell size has also been proposed as a phytoplankton functional group trait (Cloern, 2018; Gallego et al., 2019), with a consensus that smaller phytoplankton (e.g. picocyanobacteria) have lower nutritional requirements and, thus, may outcompete species with large cells when nutrients are strongly limiting (Andersson et al., 2015; Callieri & Stockner, 2000). Picocyanobacteria have traditionally received less attention than larger cyanobacteria species, partly because previous work has incorrectly assumed that species within this group do not produce toxins (Jasser & Callieri, 2017).

The aim of this research was to identify correlations of cyanobacterial community diversity, succession and dominance with environmental variables using long-term monitoring data from three important Australian drinking water reservoirs. These reservoirs provide a range of trophic levels, morphological characteristics (e.g. surface area, maximum depth) and mixing regimes, which provide insights into the relevance of the cyanobacterial alert level framework, and management and monitoring strategies. Our focus was specifically on the drivers of, and interactions among, cyanobacteria species within phytoplankton communities.

Methodology

Locations and data

Cyanobacteria cell counts and biovolumes from three drinking reservoirs in Australia (Fig. 1) were assessed through analysis of routine monitoring data collected by water utilities responsible for their management.

Lake Wivenhoe (27° 18' S, 152° 32' E) is a eutrophic, monomictic drinking water reservoir in subtropical Southeast Queensland, Australia. It has a surface area of 109 km², maximum depth of 38 m and storage of 1,165,000 ML at full supply level (FSL). Lake Tingalpa (27° 32' S, 153° 10' E) is a shallow meso-eutrophic polymictic drinking reservoir, also located in Southeast Queensland. It has surface area of 4.7 km², mean depth of 5.3 m, and maximum storage of 13,206 ML at FSL. Lake Myponga (35° 24' S, 138° 25' E) is a meso-eutrophic monomictic drinking reservoir located in South Australia. It has a surface area of 2.8 km², maximum depth of 43.9 m and maximum storage capacity of 26,800 ML at FSL.

We analysed data from the closest sampling point to the dam wall in each reservoir. For Lake Myponga, data from a second sampling point close to the dam wall were also included when it was necessary to substitute missing data from the dam wall site. Sampling points were labelled with the first letter of the name of the reservoir followed by the number 1, with the upstream station assigned 2 in Myponga (Fig. 1).

Water quality data comprised 5 years (2014–2018) for Lake Wivenhoe, 15 years (2004–2018) for Lake Tingalpa and 12 years (2008–2019) for Lake

Myponga. Water samples were taken by integrated tube from the water surface to 5-m depth for all lakes, usually between 08:00 and 10:00 h. The sampling frequency was monthly for Lake Wivenhoe and was usually monthly for Lake Tingalpa but less frequent in some instances. In Lake Myponga, sampling frequency was weekly in summer, autumn and spring but decreased to every other month during winter.

Water quality data comprised total phosphorus (TP), filterable reactive phosphorus (PO₄³⁻-P), total nitrogen (TN), total Kjeldahl nitrogen (TKN), ammonium (NH₄⁺-N) and nitrate (NO₃⁻-N). In cases when TN or TKN was missing, they were calculated as TN = TKN + NO₃⁻-N.

Cyanobacteria data included cell counts and biovolume for the total cyanobacteria community and for individual cyanobacteria species or genera. Cell counts were estimated through microscopy. Taxonomic resolution was at species level but in several instances, resolution was limited to genus (e.g. *Raphidiopsis* spp.). Biovolume was estimated from geometric shape and size of each species or genus, including categorization of some genera by morphology (e.g. *Dolichospermum* spp. (straight) and *Dolichospermum* spp. (coiled)) or size (*Aphanocapsa* spp. < 2 µm and *Aphanocapsa* spp. > 2 µm). In some instances, biovolume measurements were not available to complement cell counts and were calculated using relationships between cell counts and biovolume for each identified cyanobacteria species or genus (Supplementary Material A). These relationships were developed using all available data from all sampling points in all three lakes over the entire study period.

Sites W1 in Lake Wivenhoe and T1 in Tingalpa were equipped with a vertical profiling system (VPS), in which an EXO2 sensor (YSI, Yellow Springs, OH, USA) measured temperature hourly at 1-m depth intervals. In Lake Myponga, a VPS was located at M2, with the VPS surface water temperature at this site closely correlated with manual surface temperature measurements at site M1 ($R^2 = 0.98$, Supplementary Material B). Temperature measurements from M2 were, therefore, extrapolated to M1. Mixers and aerators are deployed close to M1 and M2 by SA Water. These are designed to minimize vertical differences in temperature and reduce the incidence of surface cyanobacteria accumulations (see Lewis et al., 2002).

Fig. 1 Location of the three drinking water reservoirs. Blue circles indicate sampling points in the lakes, and red lines indicate the dam wall of each reservoir

Data processing and statistical analysis

Data were processed using *R* 4.0.2 (R Core Team, 2020). Data were filtered to cases where at least 90% of total cyanobacteria (TC) cell counts were discretized in individual species to assure that the identified cyanobacteria species were representative of the entire cyanobacteria community diversity.

Cyanobacteria population metrics were assessed using Shannon evenness index (H), Simpson dominance index (D) and Berger-Parker dominance index (BG) (Beisel et al., 1996; Spellerberg & Fedor, 2003) for cell counts (i.e. H_{cc} , D_{cc} and BG_{cc} , respectively) and biovolume (i.e. H_{bv} , D_{bv} and BG_{bv} , respectively).

Schmidt stability index, metalimnion depth, epilimnion temperature and hypolimnion temperature

were assessed from VPS temperature profiles using *rLakeAnalyzer* (Winslow et al., 2019). The metalimnion layer for all lakes was frequently below the vertical resolution of temperature measurements (< 0.5 m); thus, for this study, the upper and lower metalimnion depths were averaged and the result is henceforth termed metalimnion depth.

Spearman non-parametric correlation and Principal Component Analysis (PCA) were calculated using *R* 4.0.2 base functions (R Core Team, 2020). Spearman non-parametric correlation was used because data did not conform to Gaussian normal distributions and variables were not linearly correlated (Hauke & Kossowski, 2011). Measurements were standardized (mean = 0, standard deviation = 1) before testing, to avoid bias due to units specific to each variable. The

significance level adopted was $P < 0.05$. Reported correlations henceforth were significant at this level, otherwise they are stated as non-significant. Plots were generated using *corrplot* (Wei & Simko, 2017) and *factoextra* (Kassambara & Mundt, 2020) R packages.

Seasonality was assessed through categorization of samples by seasons. This study was conducted in the southern hemisphere; thus, summer is from December to February, autumn from March to May, winter from June to August and spring from September to November.

Results

Cyanobacteria dynamics and concentration

Cyanobacteria richness varied considerably among lakes. Lake Wivenhoe had the highest number of species with 65 cyanobacteria genera, followed by Lake Tingalpa (46) and Lake Myponga (15). Around 60% of the identified cyanobacteria species in the lakes were classified as unicellular picocyanobacteria ($< 2 \mu\text{m}$), while the remaining 40% were mostly colonial and filamentous species.

Dominance indices BG (Berger–Parker) and D (Simpson) were strongly positively correlated ($\rho > 0.98$) for all assessed locations (Supplementary Material C). Both indices were strongly negatively correlated with H (Shannon evenness index; $\rho < -0.99$). H values in Lake Wivenhoe were consistently higher than in Lake Tingalpa and Lake Myponga, indicating a more diverse cyanobacterial community (Table 1).

The determination of the dominant species differed between biovolume and cell counts. BG_{cc} and D_{cc} dominant species (i.e. based on cell counts) differed most from BG_{bv} and D_{bv} dominant species (i.e. based on biovolume) when cyanobacterial richness was high (e.g. Lake Wivenhoe, Fig. 2a, only BG reported), usually when picocyanobacteria contributed strongly to the BG_{cc} and D_{cc} indices at the same time that cyanobacteria with large cells contributed strongly to BG_{bv} and D_{bv} (Fig. 2b, only BG reported). Disagreement also occurred at lower frequency when large-cell cyanobacteria species were dominant (e.g. BG_{cc} dominated by *Microcystis* spp. and BG_{bv} dominated by *Raphidiopsis* spp).

All analyses of environmental drivers and intra-community correlations were conducted using biovolume as metric for cyanobacteria concentration rather than cell counts. BG_{bv} and D_{bv} dominance indices were strongly correlated ($\rho > 0.98$) so only one metric (BG) was chosen for further comparisons with environmental drivers.

Cyanobacterial richness was significantly positively correlated ($P \leq 0.05$) with total cyanobacteria biovolume for Lake Wivenhoe ($\rho = 0.480$) and Lake Myponga ($\rho = 0.181$) but not for Lake Tingalpa ($P > 0.05$). Interestingly, in all lakes, total cyanobacterial biovolume was not significantly correlated with BG_{bv} or D_{bv} . Cyanobacterial richness was positively correlated with epilimnion temperature (Lake Wivenhoe, $\rho = 0.550$; Lake Tingalpa, $\rho = 0.764$; Lake Myponga, $\rho = 0.614$) and H_{bv} (Lake Wivenhoe, $\rho = 0.843$, $P < 0.05$; Lake Tingalpa, $\rho = 0.920$; Lake Myponga, $\rho = 0.973$) and negatively correlated with dominance indices BG_{bv} (Lake Wivenhoe, $\rho = -0.671$; Lake Tingalpa, $\rho = -0.859$; Lake Myponga, $\rho = -0.573$) and D_{bv} (Lake Wivenhoe, $\rho = -0.723$; Lake Tingalpa, $\rho = -0.864$; Lake Myponga, $\rho = -0.574$).

Across the lakes, there were significant positive correlations of total cyanobacteria biovolume to nitrogen, phosphorus, epilimnion temperature and/or stratification indices (Supplementary Material C). Throughout the monitoring period, none of the lakes had median total cyanobacteria biovolume $> 0.3 \text{ mm}^3/\text{l}$ (Table 1), i.e. Alert Level 1, but all had maximum total cyanobacteria biovolume $> 4 \text{ mm}^3/\text{l}$; Alert Level 2 of the World Health Organization (WHO) guidelines (Chorus & Welker, 2021). In Lake Myponga, total cyanobacteria biovolume was positively correlated with TP ($\rho = 0.274$), TKN ($\rho = 0.276$) and TN ($\rho = 0.176$), and negatively correlated with $\text{NO}_3^- - \text{N}$ ($\rho = -0.307$). Total cyanobacteria biovolume was not significantly correlated with water temperature, Schmidt stability or metalimnion depth in this lake. Among the three lakes, Lake Myponga had the highest total cyanobacteria cell counts and biovolumes, concomitantly with the highest maximum and average TP and TN concentrations over the study period (Table 1). For Lake Tingalpa, total cyanobacteria biovolume was closely correlated with Schmidt stability ($\rho = 0.766$) and metalimnion depth ($\rho = 0.753$). In Lake Wivenhoe, total cyanobacteria biovolume was positively correlated with

Table 1 Median, standard deviation (SD), minimum and maximum values of the assessed variables from the three drinking reservoirs

	Wivenhoe				Tingalpa				Myponga			
	W1				T1				M1			
	(n = 60)				(n = 58)				(n = 572)			
	Median	SD	Max	Min	Median	SD	Max	Min	Median	SD	Max	Min
TC (10^3 cells/ml)	32.5	135.2	924	0.05	3.5	128.2	1,153	0.02	0.4	493.4	13,323	0.01
TC biovolume (mm^3/l)	0.15	1.19	4.33	0	0.03	1.03	8.71	0	0.01	29.43	796	0
Richness	6	4	16	1	2	1	7	1	1	1	4	1
H_{cc} (–)	0.83	0.17	2.06	0	0.07	0.10	1.75	0	0.00	0.11	1.08	0
D_{cc} (–)	0.51	0.18	1	0.17	0.97	0.42	1	0.21	1	0.18	1	0.35
BG_{cc} (%)	52.1	18	100	27.4	98.8	17	100	33.3	100	26	100	41.7
H_{bw} (–)	0.79	0.63	2.23	0	0.00	0.34	1.20	0	0.00	0.20	0.70	0
D_{bw} (–)	0.57	0.29	1	0.13	1	0.21	1	0.32	1	0.14	1	0.47
BG_{bw} (%)	67.5	24.9	100	21.92	100	16.4	100	38.6	100	10.8	100	50.0
Epilimnion temperature ($^{\circ}\text{C}$)	23.7	2.9	26.1	16.4	26.2	2.9	29.0	19.1	20.5	2.7	24.0	11.1
Hypolimnion temperature ($^{\circ}\text{C}$)	19.9	2.2	23.0	15.4	24.5	2.6	27.1	18.0	18.9	2.8	21.8	10.3
Metalimnion depth (m)	14.5	6.1	27.0	2.4	4.2	2.7	8.6	1.5	3.2	2.4	18.6	1.5
Schmidt stability (J/m^2)	1.5×10^8	9.7×10^7	3.5×10^8	2.0×10^7	4.0×10^1	3.9×10^1	1.4×10^1	1.2×10^1	9.5×10^0	7.5×10^0	4.5×10^1	0.7×10^0
TP (mg/l)	0.01	0.01	0.02	0	0.04	0.02	0.08	0.006	0.04	0.04	0.40	0.011
$\text{PO}_4^{3-}\text{-P}$ (mg/l)	0.003	0.002	0.009	0	0.004	0.003	0.019	0.001	0.010	0.017	0.125	0.003
TN (mg/L)	0.42	0.05	0.54	0.32	0.49	0.14	0.92	0.36	1.08	0.27	2.26	0.021
TKN (mg/l)	0.40	0.05	0.54	0.32	0.45	0.11	0.76	0.32	1.00	0.26	2.25	0
$\text{NO}_3^- \text{-N}$ (mg/l)	0.00	0.04	0.15	0	0.03	0.05	0.16	0	0.06	0.05	0.22	0
$\text{NH}_4^+ \text{-N}$ (mg/l)	0.00	0.01	0.02	0	0.01	0.02	0.06	0	0.02	0.03	0.26	0

Fig. 2 Comparison between dominant cyanobacteria species using either cell counts (BG_{cc}) or biovolume (BG_{bv}) for BG dominance index calculation at Lake Wivenhoe. **a** Relative frequency of agreement or disagreement of BG_{bv} and BG_{cc} with cyanobacterial richness, where agreement represents cases when both BG_{bv} and BG_{cc} resulted in the same species as dominant while disagreement indicates cases when dominant

species were different. Bars denote the ratio of agreement and disagreement for each cyanobacterial richness and the lines represent the trend of the ratio with increasing species richness. **b** Frequency of disagreement between BG_{cc}-dominant cyanobacteria and BG_{bv}-dominant species for cyanobacterial richness

Schmidt stability ($\rho = 0.561$), TP ($\rho = 0.323$) and TKN ($\rho = 0.464$).

Cyanobacteria succession, based on changes in BG_{bv} and BG_{cc}, showed strong seasonality in Lake Wivenhoe (Fig. 3). The larger cyanobacteria species (e.g. *Raphidiopsis* spp., *Pseudanabaena* spp. and *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg) were dominant on different occasions in this lake from late spring to early autumn, while picocyanobacteria (*Aphanocapsa* spp., *Cyanocatena* spp. and *Cyanogranis* spp.) usually dominated in winter. In Lakes Myponga and Tingalpa (Supplementary Materials D and E) cyanobacteria succession varied with season but not as strongly as in Lake Wivenhoe. In Lake Tingalpa, dominance similarly alternated between picocyanobacteria and larger cyanobacteria, but seasonal patterns were less evident.

In Lake Myponga, *Microcystis* spp. and *Dolichospermum circinale* (Rabenhorst ex Bornet & Flahault) Wacklin, Hoffmann & Komárek were the dominant species, with *Microcystis* spp. mostly dominating from late spring to mid-summer and *D. circinale* from late summer to early autumn.

Species dominance and shifts due to environmental conditions

The relationship of water temperature and nutrients to species dominance varied among the lakes. In Lake Wivenhoe, total cyanobacteria biovolume and dominance (BG_{bv}) were positively correlated with water temperature for some larger species (*Raphidiopsis* spp., *Pseudanabaena* spp. and *Planktolyngbya limnetica*).

Fig. 3 Principal Component Analysis for Lake Wivenhoe differentiated by season. Length of arrows represents how well the variable aligns with the displayed principal components. Coloured points denote the season: red = summer, yellow = autumn, blue = winter and green = spring

In Lake Tingalpa, total cyanobacteria biovolume was positively correlated with water temperature (Supplementary Material C). Total cyanobacteria cell counts were negatively correlated with nutrients (TP, $\rho = -0.580$; TN, $\rho = -0.397$; NH_4^+-N , $\rho = -0.739$; NO_3^--N , $\rho = -0.690$) and higher total cyanobacteria cell counts occurred when the BG_{bv} was elevated due to the picocyanobacteria *Aphanocapsa* spp. or *Cyanocapsa* spp. In contrast, total cyanobacteria biovolume was high during periods of *Microcystis* spp. dominance, resulting in a positive correlation between total cyanobacteria biovolume and *Microcystis* spp. BG_{bv} ($\rho = 0.561$). *Microcystis* spp. BG_{bv} was negatively correlated with picocyanobacteria BG_{bv} (BG_{bv} *Microcystis* spp. vs BG_{bv} *Aphanocapsa* spp., $\rho = -0.561$). *Microcystis* spp. BG_{bv} was usually associated with high TP (Supplementary Material D), although there were no significant correlations ($P > 0.05$) between these variables (Supplementary Material C).

In Lake Myponga, *D. circinale* or *Microcystis* spp. often dominated total cyanobacteria cell counts and biovolumes. *Microcystis* spp. and *D. circinale* succession (biovolume and cell counts) were correlated with Schmidt stability and metalimnion depth, but there was no relationship between total cyanobacteria

biovolume and Schmidt stability, metalimnion depth or water temperature (see Sect. 3.1). *D. circinale* BG_{bv} was negatively correlated with Schmidt stability ($\rho = -0.297$) and metalimnion depth ($\rho = -0.416$), while *Microcystis* spp. BG_{bv} was positively correlated with epilimnion and hypolimnion temperature ($\rho = 0.561$, $\rho = 0.575$, respectively) (Supplementary Materials C and D).

For diazotrophic species, relationships of BG_{bv} with NO_3^--N were variable, both positive and negative, e.g. $\rho = 0.383$ for *Pseudanabaena* in Lake Wivenhoe and $\rho = -0.304$ for *D. circinale* in Lake Myponga. TN was also positively correlated with BG_{bv} , with some larger cell, non-diazotrophic species such as *P. limnetica* ($\rho = 0.330$ in Lake Wivenhoe), *Pseudanabaena* spp. ($\rho = 0.382$ in Lake Wivenhoe) and *Microcystis* spp. ($\rho = 0.502$ in Lake Tingalpa; $\rho = 0.148$ in Lake Myponga). In contrast, NH_4^+-N and $\text{PO}_4^{3-}-\text{P}$ were not correlated with biovolume dominance for any of the species (i.e. BG_{bv}).

Dominance of picocyanobacteria was generally associated with lower total cyanobacteria biovolume compared with periods of dominance by large-cell cyanobacteria. This dominance coincided with lower TN and NO_3^--N concentration, lower temperature and weakly stratified waters, usually corresponding to winter. Dominance of larger cyanobacteria was commonly associated with higher total cyanobacteria biovolume, and elevated concentration of TP, TN and TKN across all lakes. In contrast to the picocyanobacteria, larger cyanobacteria BG_{bv} correlations with Schmidt stability, epilimnion temperature, metalimnion depth and cyanobacterial richness were equivocal and varied across the lakes (Table 2).

Discussion

Diversity during cyanoHABs

Dominance indices for cyanobacteria species often varied between cell counts and biovolume. Cell biovolume varies by orders of magnitude among species (Jasser & Callieri, 2017), and in our study, picocyanobacteria and larger cyanobacteria were responsible for most of the variation in dominance indices between cells and biovolume (Fig. 2). Updates in cyanobacteria alert level frameworks (Chorus & Welker, 2021) have changed threshold levels to

biovolume instead of cell counts to reflect that biovolume is a better predictor of toxicity than cell counts. Based on our results, cyanobacteria and phytoplankton diversity indexes should be calculated using either biovolume or biomass, to avoid misinterpretations of environmental outcomes (e.g. toxicity) with cell counts or relative abundance.

We focused exclusively on variations in cyanobacteria within the phytoplankton community. Cyanobacteria biovolume was not significantly correlated with any of the diversity indexes H, D or BG. Richness generally increased with total cyanobacteria biovolume in all three lakes except when there was high biovolume at Myponga. The observed increase in cyanobacteria richness by lake area is similar to previous findings of increase in local and regional zooplankton species richness with landscape area (Shurin et al., 2000). However, the limited number of assessed lakes in this study hinders further generalization. More than one cyanobacterial species was often present when Alert Level 1 cyanobacteria biovolume ($0.3 \text{ mm}^3/\text{l}$) was exceeded in Lakes Wivenhoe and Tingalpa, while in Lake Myponga monospecies dominance was commonly observed. Co-occurrence of multiple cyanobacteria species has been noted in cyanoHABs from different waterbodies and climatic regions as well as with different trophic states (e.g. Amorim et al., 2020; Chellappa & Costa, 2003; Zamyadi et al., 2021). It has been related to similarities in niche and fitness among species, mostly due to size differences (Gallego et al., 2019). We found that when picocyanobacteria dominated, larger cyanobacteria species were not present, but when larger cyanobacteria dominated, they tended to co-exist with picocyanobacterial, albeit at reduced levels. Conversely, there can be successions of cyanoHAB species that form monospecific blooms (e.g. Jiang et al., 2017; Vanderley et al., 2021). Tromas et al. (2017) analysed the diversity of the bacterial community in eutrophic Lake Champlain, Canada, through genomic sequencing and observed that the relative abundance of non-dominant cyanobacteria decreased preceding a cyanoHAB while cyanobacterial richness did not.

Cyanobacterial diversity and richness may also be related to nutrient availability, as observed in Donqian Lake, China, where a significant decrease in richness was attributed to nutrient reduction following sediment dredging (Jing et al., 2013), although decreased

recruitment from overwintering or akinete sources may be possible. Interaction with other organisms can also affect cyanobacteria diversity during cyanoHABs (Amorim & Moura, 2021; Bockwoldt et al., 2017; Chellappa & Costa, 2003), with findings of positive correlations of cyanobacteria richness with other prokaryotes (Song et al., 2017; Zhang et al., 2021), and with zooplankton grazing and fish predation (Ekvall et al., 2014; Ger et al., 2014; Lampert, 1987; Urrutia-Cordero et al., 2015). We lacked data to test such responses in our study.

Environmental correlations

Highest cyanobacteria concentrations were often observed from late spring to early autumn for all three studied lakes. Increased daily solar radiation and a shallow mixed layer depth usually increase cyanobacterial biomass in warm seasons (Chorus & Welker, 2021) while higher water temperature and cyanobacteria growth rate also contribute to such increases (Lürling et al., 2013; Robarts & Zohary, 1987), but many other, often interacting, factors can be important, such as thermal stratification and external and internal nutrient loading (Carey et al., 2012).

In our study, TP was positively correlated with total cyanobacteria biomass in Lake Wivenhoe and Myponga, supporting findings from previous studies (Carvalho et al., 2013; Rigosi et al., 2015). Shifts in cyanobacterial dominance within communities may be related to changes in TP:TN ratio (Zhang & Rao, 2012) combined with specific traits of cyanobacteria (e.g. diazotrophy; organic P and high-affinity P uptake, alkaline phosphatase activity and vertical migration) (Li et al., 2020). Rapid assimilation of P means cyanobacteria compete effectively for P against other bacteria (Chorus & Welker, 2021) and luxury storage of P can support up to four cell divisions in some cyanobacteria, which may explain the absence of correlations between $\text{PO}_4^{3-}\text{-P}$ and total cyanobacteria biovolume. Low levels of dissolved inorganic nitrogen (i.e. $\text{NO}_3^-\text{-N}$, $\text{NO}_2^-\text{-N}$ and $\text{NH}_4^+\text{-N}$) have been associated with cyanobacterial dominance, particularly diazotrophic cyanobacteria (e.g. *Dolichospermum* spp.), over other species (Ferber et al., 2004), while colonial and vacuolated non-diazotrophic species (e.g. *Microcystis*) may take up $\text{NH}_4^+\text{-N}$ from bottom waters when undergoing diel vertical migration cycles (Blomqvist et al., 1994). We found that

Table 2 Correlations of cyanobacteria grouped by species dominance and specific traits (large/picocyanobacteria and diazotrophic/non-diazotrophic) with environmental conditions for each lake

			Stratification									Cyanobacteria						Nutrients											
			Epi T			SS			Met z			TC			Rich			TP			TN			TKN			NO ₃ -N		
			W	M	T	W	M	T	W	M	T	W	M	T	W	M	T	W	M	T	W	M	T	W	M	T	W	M	T
Species dominance (biovolume based)	Cell size	Large cyanobacteria																											
		Picocyanobacteria																											
	Specific traits	Diazotrophic																											
		Non-diazotrophic																											
	Total cyanobacteria biovolume																												

Blue, red and grey cells indicate positive, negative and ‘equivocal’ (i.e. variable depending on species within the group) correlations among variables for the specified lake. White cells indicate that no significant ($P > 0.05$) correlation was observed

Epi epilimnion temperature; *SS* Schmidt stability; *Met* Metalimnion depth; *TC* total cyanobacteria biovolume; *Rich* cyanobacteria richness; *TP* total phosphorus; *TN* total nitrogen; *TKN* total Kjeldahl nitrogen; NO_3^- -N nitrate; *W* Wivenhoe; *M* Myponga; *T* Tingalpa

non-diazotrophic species were more likely to be dominant at high TN and NO_3^- -N concentrations, while *D. circinale* dominated at low NO_3^- -N concentrations, similar to previous reports in the literature (Dokulil & Teubner, 2000; Reynolds et al., 2002).

In our study, picocyanobacteria dominated in Lake Wivenhoe and Tingalpa during periods with low TN (Supplementary Material C) and multiple picocyanobacteria species frequently co-existed in Lake Wivenhoe and Tingalpa (e.g. *Chroococcales Aphanocapsa* spp., *Synechococcales Cyanocatena* spp.). Seasonal dominance or co-existence of several picocyanobacterial species has been observed in other regions when there is reduced nutrient availability (e.g. Lake Maggiore, Italy Callieri & Stockner, 2000; Northern Baltic Sea, Andersson et al., 2015; and Lajes reservoir, Brazil, Rocha et al., 2019). Picocyanobacteria have small surface area to volume ratios favouring their competitiveness in low nutrient levels cyanobacteria (Wehr, 1989). The successful consortium between *Chroococcales* (e.g. *Aphanocapsa* spp.) and *Synechococcales* (e.g. *Cyanocatena* spp.) picocyanobacteria may arise from the ability of *Synechococcales* diazotrophy and *Chroococcales* to efficiently take up the excreted nitrogen from diazotrophic cyanobacteria (Andersson et al., 2015).

Large cyanobacteria species dominated biovolume in the lakes; *Raphidiopsis* spp. in Lake Wivenhoe,

Microcystis spp. in Lake Tingalpa, and *Microcystis* spp. and *D. circinale* in Lake Myponga) and increases often occurred concomitantly with decreases in picocyanobacteria biovolume except in Lake Myponga, where picocyanobacteria were rarely detected. In subtropical Lake Wivenhoe, *Raphidiopsis* spp. dominance was positively related to stratification intensity and epilimnion temperature that can be linked to warmer climates (Borics et al., 2000; Chellappa & Costa, 2003; McGregor & Fabbro, 2000). *Raphidiopsis* spp., *P. limnetica* and *Pseudanabaena* spp. often co-existed in Lake Wivenhoe, similar to picocyanobacteria observations in several other Australian drinking reservoirs (McGregor & Fabbro, 2000) and a number of temperate lakes in Europe (Dokulil & Mayer, 1996; Padisak, 1997). This co-existence has been attributed to similar ecological adaptations of shade tolerance and high NH_4^+ -N uptake rate (Présing et al., 1996), which may lead to niche overlap. In Lake Myponga, *Microcystis* spp. and *D. circinale* successively dominated the cyanobacterial community. *Microcystis* spp. usually dominated from late spring to mid-summer while *D. circinale* usually dominated during the beginning of the cooling period in autumn. *Microcystis* spp. is slightly better adapted to higher temperatures than *D. circinale* (Bormans et al., 2005; Imai et al., 2009), while *D. circinale* can adapt to nitrogen scarcity through diazotrophy (Rigosi

et al., 2014). The early seasonal dominance of *Microcystis* spp. in Lake Myponga may be related to the combination of an increase in temperature and higher nutrient availability. Prolonged thermal stratification during summer, despite the use of aerators and mixers, may decrease nitrogen availability, as observed in other studies (Yoshikawa & Furuya, 2006) and favour the shift to dominance of *D. circinale*.

One of the limitations of our study was the limited temporal resolution of the data (i.e. based on sporadic grab samples). Limited temporal resolution may result in correlations that do not represent causation (i.e. the environmental drivers for cyanobacteria succession or blooms) because the data provide a single snapshot of a continuous and time-dependent process (Gardner, 2000), thus, requiring careful analysis and interpretation of the results taking into account previous environmental histories and knowledge on cyanobacteria ecology.

Implications for water monitoring and cyanoHAB management

Microscopy is still the most commonly employed method for monitoring cyanobacteria, despite being labourious and time consuming. Microscopic cell enumeration is often done to genus or species level, and biovolume may be obtained either directly from cell dimension measurements or indirectly from the literature. The standardization of cyanobacterial diversity analysis to biovolume or biomass units would facilitate comparison between different taxa, in accordance with a recently proposed framework for cyanoHABs management (Chorus & Welker, 2021). Our study provides a brief resource based on the assessed data, that can be used for conversion between cell counts and biovolume (Supplementary Material A) in cases where site-specific data are not available.

The choice of management strategy to mitigate cyanoHAB risk is, among other factors, dependent on the dominant cyanobacteria species or trait-based group of cyanobacteria species. For instance, the relative control of nitrogen and phosphorus may vary depending on the need to control heterocystous versus non-heterocystous cyanobacteria (Agawin et al., 2007; Hamilton et al., 2016; Wan et al., 2019). Destratification of the water column can be employed to decrease the abundance of high-light dependent and buoyant cyanobacteria species (Visser et al., 2016), but long-

term effects of this control should take into account adaptive features of cyanobacteria (e.g. Antenucci et al., 2005). Dosage of algicides to control cyanobacteria may vary according to the dominant species. In cases where colony-forming taxa dominate, higher dosages may be required because mucilage hinders the oxidizing effect of the algicide (Lürling et al., 2014). Application of algicides should be controlled since persistent use of algicides may favour the selection of resistant cyanobacteria species (Rouco et al., 2014), besides increasing the potential for impacts on other phytoplankton groups (Matthijs et al., 2012). The effectiveness of biomanipulation has been shown to vary according to the susceptibility of cyanobacteria to predation (Urrutia-Cordero et al., 2016), sometimes associated with the presence of toxic colony-forming or filamentous species (Vanderploeg et al., 2001), and the ability to concurrently reduce nutrient loads (Peretyatko et al., 2012). Cyanobacteria removal in drinking water treatment plants is also specific to the species and the treatment process (Pazouki et al., 2016; Zamyadi et al., 2021). Cases where multiple cyanobacteria species co-exist and successively dominate, as observed in our results for Lakes Wivenhoe and Tingalpa, pose an increased challenge for drinking water treatment plant operators (Zamyadi et al., 2013) and control strategies are often set at genus level.

Identification and quantification of cyanobacterial community composition in a fast, reliable and cost-efficient manner is crucial for proactive cyanoHAB management. Genomic and molecular based methods (see Moreira et al. 2014 for a review) provide a detailed characterization and quantification of cyanobacterial taxa beyond morphological-based enumeration and classification, and include identification of toxic strains (D'Agostino et al., 2016), but can be costly. Flow cytometry may also allow rapid quantification of cyanobacteria abundance and biovolume, including in situ deployments (Havlik et al., 2013; Pomati et al., 2013) and reduced bias in biovolume estimates by negating use of chemical preservatives for cell storage or immobilization (Hawkins et al., 2005). Recent machine learning applications may allow flow cytometry to differentiate phytoplankton to species level, including for cyanobacteria. For instance, convolutional neural networks, a deep learning technique, were employed to differentiate 80 diatoms species (Pedraza et al., 2017) with 99.5% of accuracy when flow cytometry training samples are

large. Samples with *Microcystis aeruginosa*, *Microcystis wesenbergii*, *Oscillatoria* sp., *Aphanizomenon* sp. and *Dolichospermum* sp. have been systematically classified and enumerated using similar deep learning algorithms combined with flow cytometry (Baek et al., 2020). Other machine learning applications have been used to optimize flow cytometry measurements, including biovolume and cell counts of phytoplankton functional groups (Thomas et al., 2018), with high quantitative similarity between flow cytometry and microscopy estimates.

Other technologies, based primarily on sensors tuned to optical properties of phycocyanin or phycoerythrin, can provide high temporal and spatial resolution of cyanobacteria biomass in real time and should be calibrated against cyanobacteria biovolume rather than cell counts (Rousso et al., 2022; Bertone et al., 2018, 2019). These sensors may be useful for proactive cyanoHAB management but trade off precision (e.g. species or taxon resolution) and potentially accuracy (e.g. due to interferences) against rapid population-level biomass assessment. Hyperspectral remote sensing focusing on phycocyanin reflectance can provide high cost-efficient spatial estimates of total cyanobacteria over extended areas. However, it also does not differentiate cyanobacteria to species level and requires careful species-specific validation and ground truthing based on direct measurements of biomass. Cyanobacteria communities are often composed by multiple species, which should be reflected in the calibration of optical sensors and, where possible, use of multiple cross-validation methods. Optimization of fluorescence sensors through machine learning can assist in this field of research, including detection of anomalies to trigger management responses (Almuhtaram et al., 2021) and correction of light-induced fluorescence quenching (Lucius et al., 2020; Rousso et al., 2021). The application of machine learning techniques to predict cyanobacteria species dominance based on environmental conditions has been suggested as a way to improve calibration of fluorescence sensors and to provide species-specific information in real time to support improved cyanoHAB management (Rousso et al., 2020). This approach would still rely on species identification through other methods and comprehensive historical data to develop predictive models. Nevertheless, as highlighted by Simis et al. (2007), some monitoring methods have intrinsic limitations and we should aim

to strategically complement them. Comprehensive cyanoHABs monitoring plans should, therefore, encompass a range of methods aiming to integrate precise strains and species identification to support species-targeted responses, and autonomous methods that generally provide community level assessments and allow fast and proactive responses from water managers.

Conclusions

An analysis of long-term routine monitoring data from three Australian drinking reservoirs was conducted to examine relationships of cyanobacteria intra-community diversity and dominance to water quality and stratification parameters. Diversity analysis of cyanobacteria populations quantified dominance indexes using species cell counts or biovolume. Cell counts for cyanobacterial dominance calculations result in overestimation of picocyanobacteria dominance over other cyanobacteria due to their small cell size. We recommend that biovolume or biomass is used for phenological assessments of cyanobacteria, which aligns with recent Alert Level Frameworks for cyanoHABs assessment risk.

The two subtropical lakes included in this study had higher cyanobacterial diversity than the lake in the temperate region. In the subtropical lakes, picocyanobacteria (*Aphanocapsa* spp., *Cyanocatena* spp. and *Cyanogranis* spp.) and large-cell, colonial and filamentous cyanobacteria (*Raphidiopsis* spp., *Pseudanabaena* spp., *Microcystis* spp.) often had alternate periods of dominance, with picocyanobacteria dominant when nutrients were low, and colonial and filamentous cyanobacteria dominant during warmer, nutrient-rich conditions, particularly when phosphorus concentrations were higher. In temperate Lake Myponga with lower cyanobacterial diversity, *Microcystis* spp. dominated during warm and nitrogen-rich conditions, followed by *D. circinale* in late summer as nitrogen concentrations and water temperature decreased. Among larger cyanobacteria species, non-diazotrophic species dominated during periods with high inorganic N and diazotrophic species dominated at low N concentrations. Total cyanobacteria biovolume tended to be higher when water temperature and total phosphorus concentrations were elevated. Our results indicate that reduction of nutrient loading in

lakes may reduce total cyanobacteria concentration and favour a shift to picocyanobacteria, but targeted reductions of nitrogen and phosphorus should be considered as they could affect the abundance and proportions of non-diazotrophic and diazotrophic species.

Cyanobacteria richness frequently increased with total cyanobacteria biomass, indicating that multiple species can co-exist during cyanoHABs, which challenges targeted species-specific management responses. CyanoHABs management should encompass comprehensive monitoring plans that provide adequate temporal, spatial and taxa precision to support targeted and proactive prevention or treatment responses. Analysis of routine monitoring data in our study can support a site-specific understanding of cyanobacteria dynamics, which is crucial for cyanoHAB prevention and mitigation, but combinations of one or more monitoring methods with machine learning applications could be used to optimize species-specific cyanoHAB management.

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Data availability Not applicable.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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