

## Trophic interactions promote dominance by cyanobacteria (*Anabaena* spp.) in the pelagic zone of Lower Karori Reservoir, Wellington, New Zealand

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**Abstract** Cyanobacterial blooms have occurred in the Lower Karori Reservoir (Wellington, New Zealand) since 2000, resulting in reduced water quality and potential health risks. This study examined the factors that contribute to the cyanobacterial blooms in the reservoir (October 2003 to July 2004). In particular, it examined how thermal stratification influences the chemical dynamics in the reservoir, and the potential cascading effect of zooplanktivorous perch (*Perca fluviatilis*) in promoting high phytoplankton biomass. Thermal stratification, coupled with increased water column stability occurred from October to March. Oxygen levels were reduced in the hypolimnion during stratification. Nutrient concentrations declined during stratification and became elevated after the collapse of the bloom in February 2004. Concentrations of *Anabaena lemmermannii* increased with the onset of thermal stratification. Zooplankton abundance peaked during stratification and consisted mainly of rotifers. The perch caught during this study were typically small-sized individuals, which had consumed mostly large-sized zooplankton. The development of cyanobacterial blooms in the Lower Karori Reservoir is probably owing to a combination of factors including low nitrogen concentrations that favour nitrogen-fixing cyanobacteria and the ability of cyanobacteria to adjust their buoyancy and maintain their position in the water column

during thermal stratification. Predation by perch probably maintains large zooplankton species at low densities and consequently reduces grazing pressure on phytoplankton populations.

**Keywords** cyanobacteria; *Anabaena*; phytoplankton; zooplankton; thermal stratification; nitrogen; phosphorus; *Perca fluviatilis*

### INTRODUCTION

Cyanobacterial blooms in freshwater lakes are a problem worldwide and have increasingly become extensively studied owing to negative economic and recreational impacts (e.g., Steffensen et al. 1999). Dominance by cyanobacteria in freshwater pelagic food webs can be attributed to many factors including the ability of some species to fix atmospheric nitrogen and thus use low nitrogen to phosphorus ratios (Smith 1983), buoyancy regulation (Reynolds et al. 1987), and reduced zooplankton grazing compared with other phytoplankton species (de Bernardi & Giussani 1990).

Two environmental factors that are thought to promote the succession of phytoplankton communities towards dominance by cyanobacteria are thermal stratification and nutrient availability (Reynolds 1984). Grazing by zooplankton has been shown to influence the succession towards dominance by cyanobacteria (Sterner 1989). Zooplankton can exert direct effects on phytoplankton community structure through grazing as well as indirect effects through nutrient recycling (Lehman & Sandgren 1985; Bergquist & Carpenter 1986; Sterner 1986). However, studies investigating the ability of zooplankton to consume cyanobacteria have been inconclusive (e.g., de Bernardi & Giussani 1990). Toxins from cyanobacteria have been shown to affect herbivores (Christoffersen & Burns 2000) and some cyanobacteria could be difficult to consume owing to the shape and size of large colonies (Webster & Peters 1978; Porter & McDonough 1984). A popular theory is that zooplanktivorous fish may promote

phytoplankton blooms by reducing the abundance and size of herbivorous zooplankton that would normally prey upon the phytoplankton (Brooks & Dodson 1965; Shapiro et al. 1975).

European perch (*Perca fluviatilis* L.) populations in New Zealand are generally characterised by large populations of small fish (Duncan 1967) despite their potential to reach large size (up to 3 kg) (Jellyman 1980). These populations of small fish are probably the result of a combination of factors including the absence of significant predators (McDowall 1990), high intraspecific competition (Duncan 1967), and a lack of food sources (Deelder 1951). Under such conditions, perch are known to form stunted populations consisting primarily of small fish (Alm 1946).

The Lower Karori Reservoir (41°17'33.25"S, 174°45'05.69"E) is within a 252 ha catchment of mixed regenerating shrub-hardwood forest encompassing two dams that were part of the first water supply scheme for Wellington City (Lynch 1995). The Lower Karori Reservoir has an average depth of 8.2 m, a maximum depth of c. 20 m and a total area of 0.025 km<sup>2</sup> (K. Calder unpubl. data). The catchment has been closed off to the public since 1906 when it was used mostly for farming. The Karori Wildlife Sanctuary Trust was formed in 1995 with the aim to create a pest-free "island" on the mainland. An 8.6 km predator-proof fence surrounding the catchment was completed in 1999. Exotic species management and eradication programmes continue within the sanctuary. Two introduced species of freshwater fish are found in the reservoir, brown trout (*Salmo trutta*) and European perch. Perch were introduced into the dam in 1878 by the Wellington Acclimatisation Society (Thomson 1922). Juvenile perch are known to be zooplanktivorous both in New Zealand (Duncan 1967) and in their native Europe (Smyly 1952).

The first known severe cyanobacterial bloom occurred in the Lower Karori Reservoir during the summer of 2000/01 (K. Calder unpubl. data). The dominant bloom-forming species in the reservoir were *Anabaena lemmermannii* and *A. circinalis* (Wood 2005). In January 2003, anatoxin-a was detected in a bloom sample from the Lower Karori Reservoir (Wood et al. 2006). These blooms have many detrimental effects on the sanctuary operations, in particular the potential health effects of toxin production. In this study we aimed to examine the factors that contribute to the cyanobacterial blooms in the Lower Karori Reservoir. In particular, we examined how the hydrodynamics and chemistry of

the lake influence the phytoplankton community, and the potential cascading effect of zooplanktivorous perch (*Perca fluviatilis*) in promoting high phytoplankton biomass.

## MATERIALS AND METHODS

Water column samples were taken at regular intervals between 7 October 2003 and 7 July 2004. Samples were taken monthly or fortnightly during the winter and weekly during the summer months, from three randomly placed permanent sampling stations and from three depths (2, 6, and 10 m) at each station with a transparent 2-litre self-activating plankton trap (Schindler 1969). Two litres of water were collected at each sampling point and taken to the laboratory within 2 h of collection for further analysis and preservation. Water temperature and dissolved oxygen were measured in the field with an YSI Model 58 meter (YSI Environmental, Yellow Springs, Ohio, United States) at 1-m depth intervals from the surface to 10 m and at 2-m intervals from 10 m to 16 m. From February 2004 to June 2004, dissolved oxygen was not recorded owing to equipment failure. Water transparency was measured in the field at the three sites with a black and white Secchi disc (Bartram & Ballance 1996) and pH was measured in the laboratory with a Metrohm Herisau E488 pH meter (Metrohm Ltd, Herisau, Switzerland).

Gill net sampling for perch (*Perca fluviatilis*) began on 23 December 2003 and continued until 4 May 2004. A 30-m gill net with 6-m panels and mesh sizes of 20, 25, 50, 75, and 100 mm with a width of 1.5 m was used. On weekly occasions the net was set overnight for c. 15 h. Live fish were euthanised by way of pithing. Captured fish were measured (total length, to the nearest mm), weighed and immediately frozen for later analysis. Stomach contents of all fish were examined under a dissecting microscope at 40× magnification. All food items were identified to the lowest taxonomic level possible and counted.

To estimate phytoplankton abundance, 50 ml subsamples were preserved with Lugol's solution (Hotzel & Croome 1999) and cell counts performed using an inverted microscope and a sedimentation chamber (Utermöhl 1958). The whole chamber was scanned at 200× magnification. The total counts were standardised to cells ml<sup>-1</sup>. Cyanobacteria were identified to species level and other phytoplankton taxa were identified to genus level with reference to Entwistle et al. (1997), Biggs & Kilroy (2000),

Moore (2000), and Baker & Fabbro (2002). A 500 ml subsample was preserved with 4% borax-buffered formalin and used to estimate zooplankton abundance. The total number of individuals in a 500 ml subsample was counted and standardised to individuals litre<sup>-1</sup>. Organisms were counted and identified to the lowest possible taxonomic group using a dissecting microscope with reference to Chapman & Lewis (1976) and Shiel (1995).

Water for dissolved nutrient analyses was filtered through 47 mm diameter Whatman GF/C glass microfibre filters that were pre-washed with distilled water. Filtered water was stored frozen in clean polyethylene bottles until analysis. Nitrate, nitrite, ammonium, and soluble reactive phosphorus (SRP) concentrations were determined using an Aqua Analyser (Orbeco-Hellige model 952, Farmingdale, New York, United States).

Repeated measures analysis of variance was used to compare the effect of depth on plankton abundance and distribution, nutrient concentrations, and pH levels using SPSS 11.15 for Windows (SPSS Inc., Chicago, United States). All statistical analyses were performed on  $\log(x + 1)$  transformed data to homogenise the variances where  $x$  is a single data point. The possibility of a Type I error occurring when a number of tests is performed on the same data set is high. So for all tests,  $P$  values  $<0.01$  were considered to be statistically significant as a result of a Bonferroni adjustment.

Water column stability (potential energy anomaly,  $J/m^2$ ) was calculated using MATLAB<sup>®</sup> software (Mathworks Inc., Massachusetts, United States) using the following formula:

$$\text{Potential energy anomaly} = \rho \times g \times (H_{\text{mixed}} - H_{\text{stratified}})$$

where  $\rho$  is the average density of the water column,  $g$  is the gravitational constant (i.e., 9.81),  $H_{\text{mixed}}$  is the height of the centre of mass of the water column from the lakebed (i.e., half the water column depth), and  $H_{\text{stratified}}$  is the height of the centre of mass of the water column from the lakebed when the lake is stratified. To compare relative plankton species abundances during times of stratification (increased water column stability) and times of complete mixing (low water column stability), plankton species abundance values were averaged over time to produce a site value. The period of increased water column stability used for the analysis was between 12 November 2003 and 28 January 2004. The low water column stability period used was between 6 April 2004 and 7 July 2004.

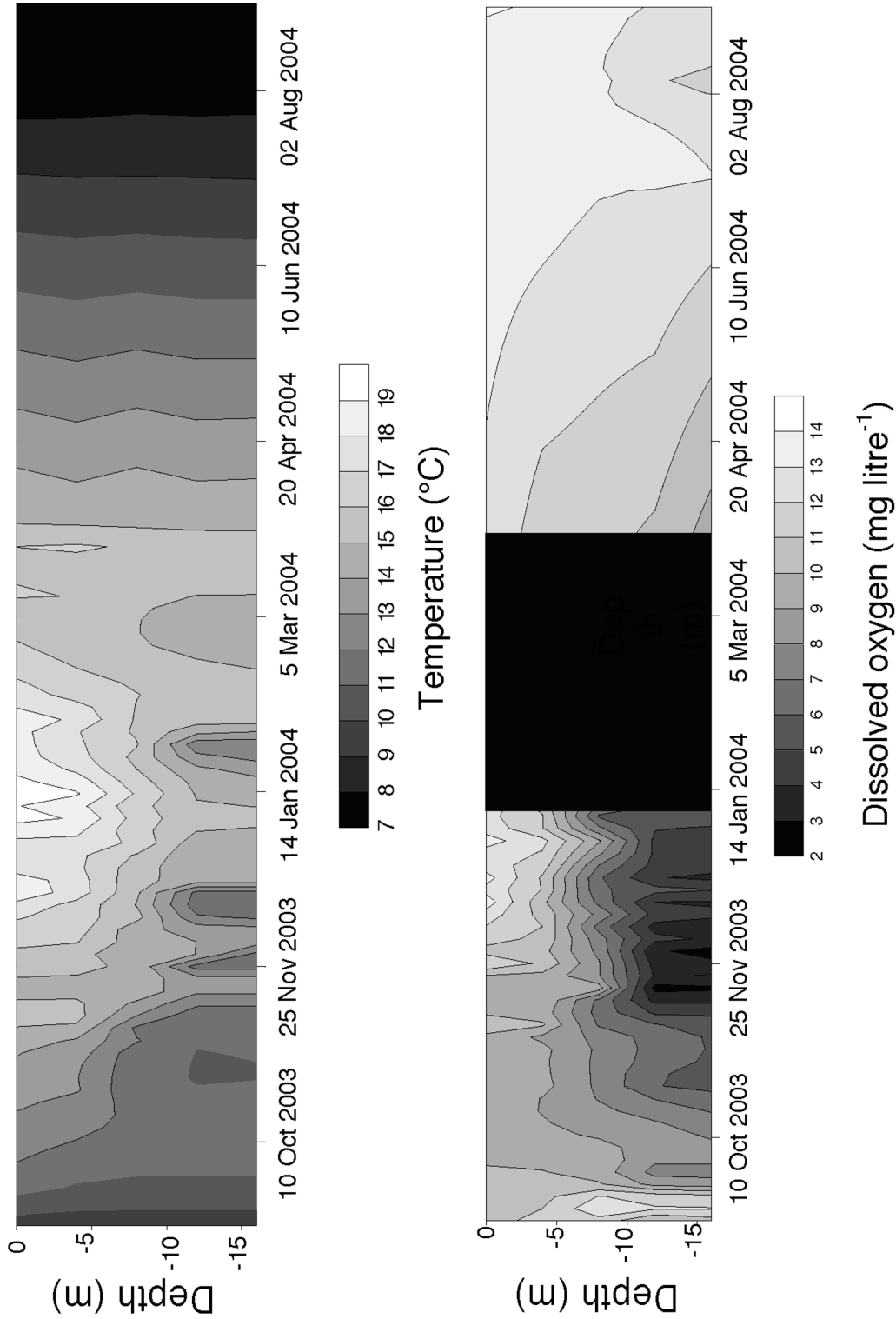
Non-metric multidimensional scaling (MDS, using the Bray-Curtis dissimilarity coefficient) using PRIMER 5 (PRIMER-E Ltd, Plymouth, United Kingdom) on  $\log(x + 1)$  transformed data was used to compare relative plankton species abundances during the two periods (Clarke & Warwick 2001). A two-way nested analysis of similarities (ANOSIM) with depth and stratification as factors was used to test for similarity of plankton species composition during the two periods. These analyses are commonly used to examine similarities between species assemblages (e.g., Van der Gucht et al. 2005).

## RESULTS

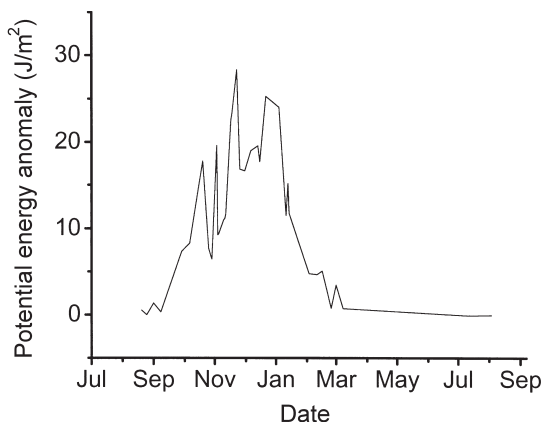
### Physical and chemical dynamics

The Lower Karori Reservoir began to thermally stratify in November 2003, and ended in March 2004 (i.e., temperature varied greater than 2°C from the surface to bottom waters during this time) (Fig. 1A). After March there was little variation in temperature throughout the water column. The strongest stratification occurred in January, when surface temperatures reached 20°C and temperatures in the hypolimnion were 12°C. Thermal stratification was associated with reduced concentrations of dissolved oxygen in the hypolimnion (lowest value c. 3.8 mg litre<sup>-1</sup>, 11 December 2003) (Fig. 1B). During the winter months the lake was homothermous with temperatures below 10°C and had high dissolved oxygen levels (above 12 mg litre<sup>-1</sup>) throughout the water column. Water column stability increased over the summer months as the water thermally stratified (Fig. 2). The degree of water column stability varied greatly from October 2003 to February 2004 but the water column did not completely re-mix during this period.

All nitrogen species decreased slightly from November to January (Fig. 3A). Concentrations of ammonium and nitrate increased sharply in January. Concentrations of nitrogen species did not differ significantly with depth ( $P_{\text{ammonium}} = 0.971$ ,  $P_{\text{nitrate}} = 0.998$ ,  $P_{\text{nitrite}} = 0.552$ ) (Table 1). Nitrite concentrations were very low and ammonium was the most abundant form of nitrogen. SRP had a mean of 0.02 mg litre<sup>-1</sup> and showed considerable temporal and spatial variation (Fig. 3B). SRP concentrations changed significantly over time ( $P = 0.004$ ) and with depth ( $P = 0.008$ ) (Table 1). Concentrations were generally highest in the samples at 10 m and lowest at 2 m. SRP levels were lowest at all depths during stratification and the greatest variation



**Fig. 1** A, Temperature (°C) and B, dissolved oxygen (mg litre<sup>-1</sup>) depth profiles for the deepest station at Lower Karori Reservoir, Wellington, over the 9-month study period (2003–04). Temperature and dissolved oxygen were measured at 1-m intervals from the surface to 10 m and at 2-m intervals from 10 m to 16 m. No readings from February to June when the oxygen meter malfunctioned.

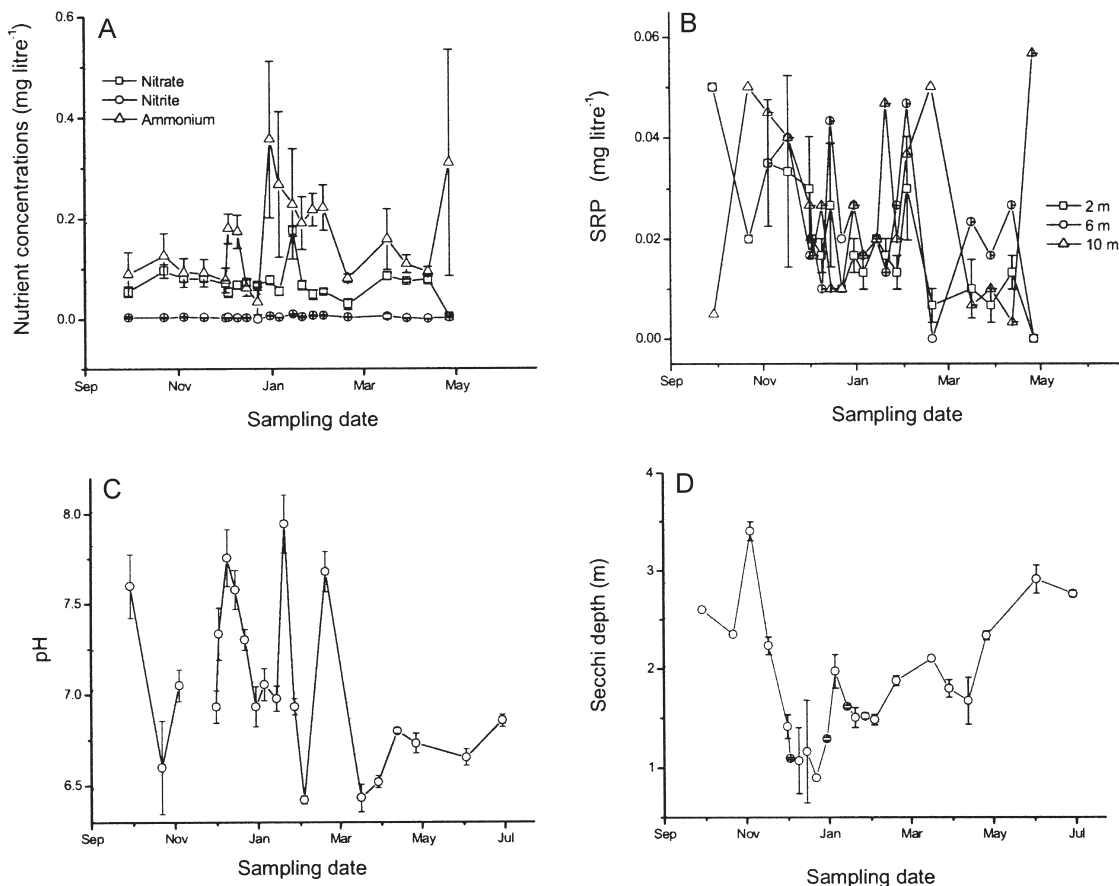


**Fig. 2** Lake water column stability (potential energy anomaly,  $J/m^2$ ) of the Lower Karori Reservoir, Wellington, over the 9-month sampling period in 2003–04.

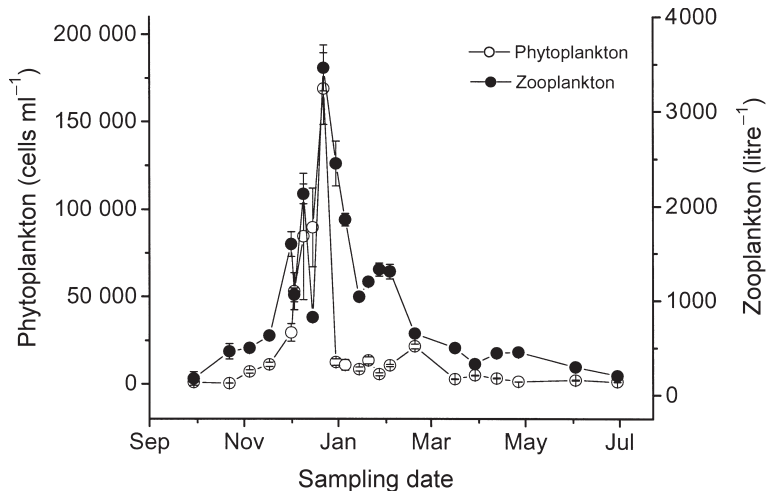
between depths occurred during April when there was little variation in temperature throughout the water column. The pH fluctuated greatly with a range between 6.10 and 8.25 (Fig. 3C). Secchi disc depth ranged between a maximum of 3.40 m (12 November 2003) and a minimum of 0.90 m (30 December 2003) (Fig. 3D).

**Phytoplankton and zooplankton communities**

Phytoplankton abundance peaked at the end of December ( $170\,000\text{ cells ml}^{-1}$ ) (Fig. 4). Cyanobacteria concentrations did not differ with depth throughout the sampling period ( $P = 0.481$ , Table 1) and constituted almost all the peak phytoplankton density on 30 December 2004 (Fig. 5). Four species of *Anabaena* were present in the Lower Karori Reservoir during the



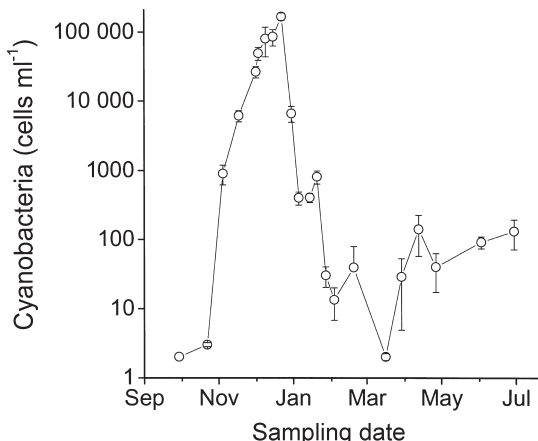
**Fig. 3** **A**, Nitrogen species concentrations ( $mg\ litre^{-1}$ ); **B**, soluble reactive phosphorus (SRP) concentrations ( $mg\ litre^{-1}$ ); **C**, pH; and **D**, Secchi disc depth (m) for the 9-month sampling period (2003–04) in the Lower Karori Reservoir, Wellington. Values ( $\pm 1\ SE$ ) were averaged, concentrations are shown for each depth averaged over the three sites as these differences were significant.



**Fig. 4** Total phytoplankton (cells ml<sup>-1</sup>) and total zooplankton (no. litre<sup>-1</sup>) counts (mean ± 1 SE) for the 9-month period (2003–04) in the Lower Karori Reservoir, Wellington.

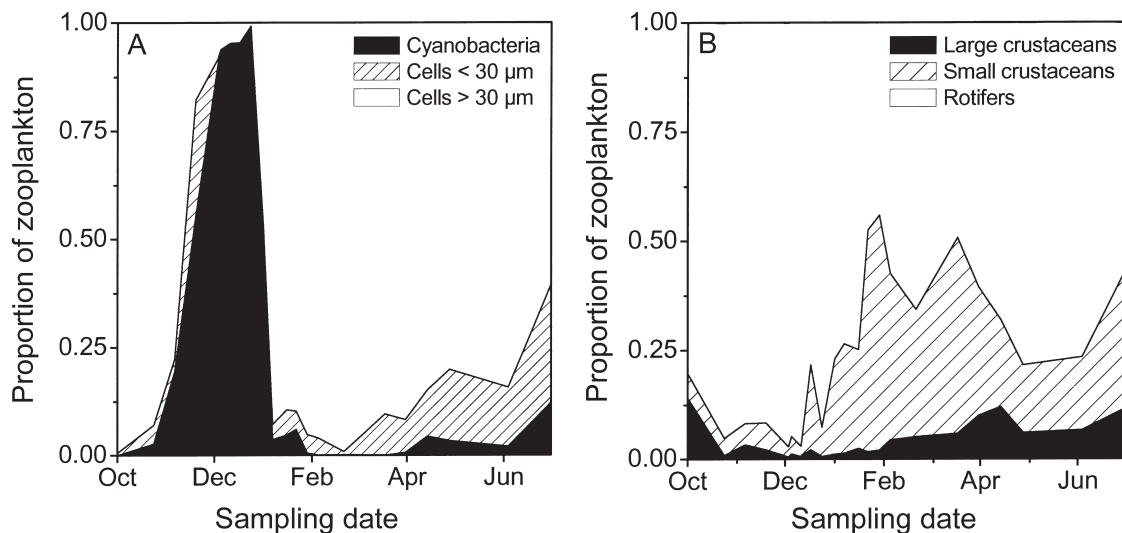
**Fig. 5** (below) Cyanobacteria (cells ml<sup>-1</sup>) counts (mean ± 1 SE) for the 9-month sampling period (2003–04) in the Lower Karori Reservoir, Wellington, averaged across all depths and sites.

sampling period (Table 2). Throughout the summer months the dominant species was *A. lemmermannii*, with *A. circinalis* and *A. cf. inaequalis* at lower densities. *Anabaena cf. planktonica* was recorded for the first time in the Lower Karori Reservoir on 4 February 2004 and stayed at low densities throughout the remainder of the sampling period (Table 2). Cyanobacteria dominated the samples during early summer but populations declined rapidly at the beginning of January 2004 (Fig. 6A). Total phytoplankton counts did not differ between depth samples ( $P = 0.267$ ) (Table 1). Large phytoplankton species (i.e., species >30 μm) constituted the greatest proportion of phytoplankton in the samples, particularly during the spring. Common species



**Table 1** Results of repeated measures ANOVA on log(x + 1) transformed data to determine the effects of depth and time on nutrient concentrations, pH levels, and plankton abundance. Values are *P* values with corresponding *F* statistics (d.f.<sub>depth</sub> = 2; d.f.<sub>time</sub> = 21; d.f.<sub>time × depth</sub> = 42). To avoid a Type I error, a Bonferroni adjustment was performed on all tests as they were from the same data set (i.e., 0.05 / 8 (no. of tests) c.  $P < 0.01$ ).

	Between subjects effects		Within subjects effects			
	Depth		Time		Time × Depth	
	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>
Nitrate	0.998	0.002	0.000	17.830	0.890	0.673
Nitrite	0.552	0.656	0.000	3.123	0.160	1.319
Ammonium	0.971	0.030	0.113	1.525	0.759	0.794
Soluble reactive phosphorus	0.008	546.849	0.004	2.396	0.000	2.456
pH	0.193	2.188	0.000	45.634	0.353	1.099
Cyanobacteria	0.481	0.828	0.000	55.420	0.715	0.855
Total phytoplankton	0.267	1.656	0.000	45.477	1.000	0.353
Total zooplankton	0.642	0.477	0.000	40.487	0.980	0.534



**Fig. 6** Seasonal changes in abundance of **A**, phytoplankton and **B**, zooplankton groupings in the Lower Karori Reservoir, Wellington, represented as a proportion of total phytoplankton and zooplankton abundance, respectively.

**Table 2** Plankton taxa recorded in the Lower Karori Reservoir, Wellington, during the 9-month sampling period (2003–04). Taxa are listed in order of abundance over the entire monitoring period.

Phytoplankton	Zooplankton
<i>Anabaena lemmermanii</i> P. Richt	<i>Keratella</i> spp. Bory de St. Vincent
<i>Volvox</i> sp. (Linnaeus) Ehrenberg	cf. <i>Polyarthra</i> spp. Ehrenberg
<i>Anabaena circinalis</i> Rab.	<i>Bosmina meridionalis</i> Sars
<i>Anabaena</i> cf. <i>inaequalis</i> (Kützing)	cf. <i>Trichocerca</i> sp. Lamarck
Bornet & Flahault	Copepod nauplii
<i>Aulacoseira</i> sp. Thwaites	cf. <i>Filinia</i> sp. Bory
<i>Asterionella</i> sp. Hassal	<i>Asplanchna</i> sp. Gosse
<i>Closterium</i> sp. Nitzsch ex Ralfs	Calanoid copepods
<i>Staurastrum</i> sp. [Meyen] Ralfs	Cyclopoid copepods
<i>Dictyosphaerium</i> sp. Nägeli	<i>Daphnia</i> cf. <i>carinata</i> King
<i>Trachelomonas</i> sp. Ehrenberg	Chydoridae sp.
Naviculoid diatoms	Acarina spp.
<i>Anabaena</i> cf. <i>planktonica</i> Brunnthaher	Ostracod spp.
<i>Cryptomonas</i> sp. Ehrenberg	<i>Ceriodaphnia</i> cf. <i>dubia</i> Richard
<i>Oocystis</i> sp. A. Braun	
<i>Peridinium</i> sp. Ehrenberg	
<i>Scenedesmus</i> sp. Meyen	
<i>Cosmarium</i> sp. Corda ex Ralfs	

were *Volvox* sp. and *Asterionella* sp. With the onset of thermal stratification these species were quickly replaced by *Anabaena* spp. Small phytoplankton, such as *Trachelomonas* sp. and *Staurastrum* sp., increased in relative abundance during the winter, but did not dominate samples.

Total zooplankton abundance peaked at the end of December at c. 3500 individuals litre<sup>-1</sup> (Fig. 4),

with no significant difference between depths ( $P = 0.642$ , Table 1). Rotifers were the most common zooplankton taxa during this peak and constituted 90% of species during this time. Rotifers were the most frequently recorded zooplankton taxa throughout most of the sampling period (Fig. 6B). Common taxa were *Asplanchna* sp. and *Keratella* spp. (Table 2). Crustaceans became more

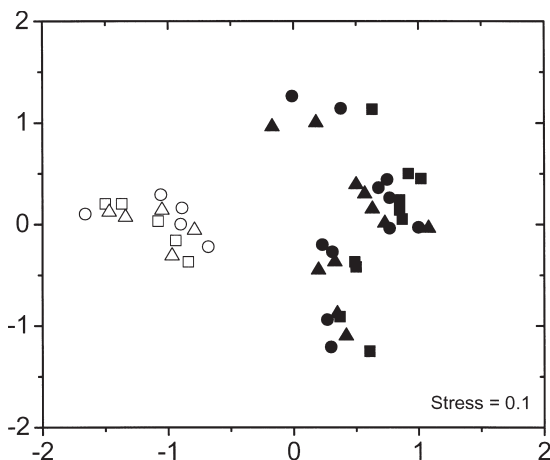
dominant through the winter, particularly small crustaceans such as *Bosmina meridionalis*. Three species of limnetic Cladocera were recorded in the reservoir, *B. meridionalis*, *Daphnia cf. carinata*, and *Ceriodaphnia cf. dubia*. *Bosmina meridionalis* was the most abundant crustacean during the entire period. Large crustaceans were consistently present at low densities, e.g., *Daphnia cf. carinata* abundance was usually less than five individuals litre<sup>-1</sup>. The slightly smaller *Ceriodaphnia cf. dubia* was less abundant. Chydorid species occurred in samples regularly. Copepods were more common than cladocerans with both calanoid and cyclopoid species present.

The abundance of cyanobacteria, total phytoplankton, and total zooplankton all varied significantly over time ( $P$  values  $< 0.001$ , Table 1). Testing did not show a significant time  $\times$  depth interaction (Table 1), indicating similar plankton abundances throughout all depth layers in the reservoir during the entire sampling period.

ANOSIM analyses showed that the period of thermal stratification (increased water column stability) was associated with changes in plankton species composition (Fig. 7). Relative species composition differed significantly between times of increased water column stability and times of complete water column mixing (Global  $R = 0.741$ ,  $P = 0.001$ ), whereas no relationship was found between the distribution and abundance of plankton species and depth during either periods (Global  $R = -0.091$ ,  $P = 1.00$ ). Both phytoplankton and zooplankton abundance peaked during increased water column stability and were low when the water column was completely mixed.

#### Perch size structure and diet

The perch (*P. fluviatilis*) population in the Lower Karori Reservoir was characterised by a large abundance of small, juvenile fish. Ninety-five of the 100 perch caught were between 60 and 110 mm total length (Fig. 8A). Total lengths of the five larger perch were between 140 and 190 mm. The consumption of zooplankton appeared to be strongly related to the size of the perch (Fig. 8B), with zooplankton being the main source of food for the small fish. Large sized perch showed no evidence of having consumed zooplankton, although the sample size was small. These large perch mostly had empty stomachs but some had been consuming terrestrial invertebrates (e.g., larvae from the Geometridae family). The diet of smaller perch consisted of both zooplankton (pelagic invertebrates) and benthic invertebrates



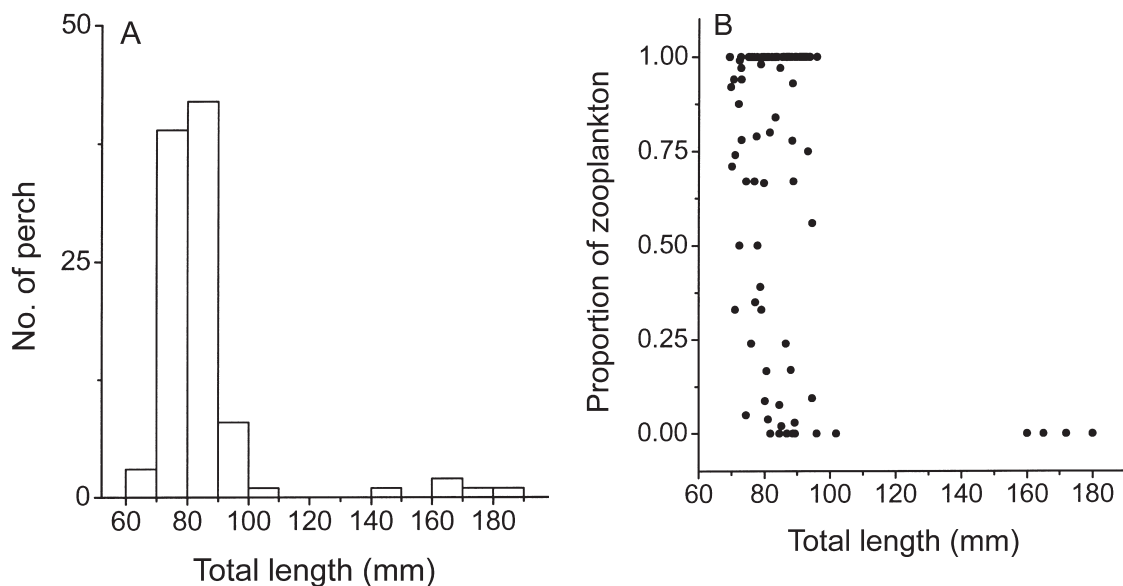
**Fig. 7** Non-metric multidimensional scaling (Bray-Curtis dissimilarity) on  $\log(x + 1)$  transformed data of relative species composition during periods of thermal stratification and complete water column mixing in the Lower Karori Reservoir, Wellington. (Closed squares, 2m, stratification; open squares, 2m, no stratification; closed circles, 6m, stratification; open circles, 6m, no stratification; closed triangles, 10m, stratification; open triangles, 10m, no stratification).

(Fig. 9). Four main taxa of zooplankton were consumed; *Daphnia cf. carinata*, *Ceriodaphnia cf. dubia*, cyclopoid copepods, and calanoid copepods. *Daphnia cf. carinata* was the most commonly consumed taxon, particularly during the autumn. During the summer, copepods were more frequently consumed. The previously mentioned four taxa were the largest zooplankton taxa sampled from the lake during the study. Benthic invertebrates were also an important food source, especially during the summer months. Almost all of the benthic invertebrates consumed were chironomid (midge) larvae.

## DISCUSSION

### Effects of thermal stratification on the phytoplankton community

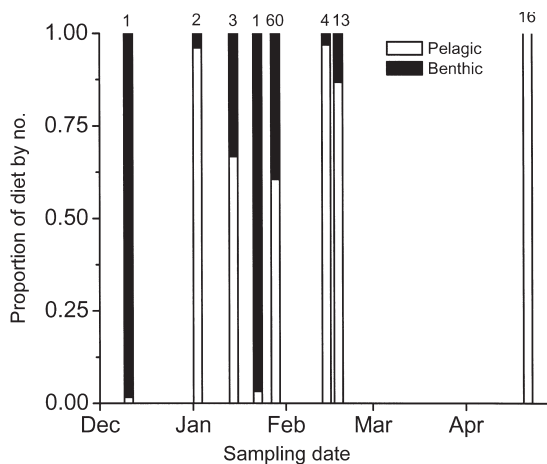
A common occurrence in deep temperate lakes is the succession of phytoplankton from diatoms and green algae to cyanobacteria in summer with the development of thermal stratification (Oliver & Ganf 2000). The onset of thermal stratification in the Lower Karori Reservoir during November/December coincided with changes in phytoplankton



**Fig. 8** Size and diet of perch (*Perca fluviatilis*) in the Lower Karori Reservoir, Wellington. **A**, Length distribution of perch caught over the 5-month sampling period (2003–04). **B**, Proportion of stomach contents that were zooplankton in relation to size of perch.

species composition. Green algae (e.g., *Volvox* sp., *Staurastrum* sp.), and diatoms (e.g., *Asterionella* sp., *Aulacoseira* sp.) were the dominant taxa during the isothermal period. Cyanobacterial densities (mainly *A. lemmermannii*) increased once the water column stratified in December and, at their peak, cyanobacteria represented over 99% of cell densities. *Anabaena lemmermannii* is known to form blooms in other New Zealand lakes (Wood 2005). The bloom in the Lower Karori Reservoir was short-lived and collapsed at the beginning of January, and was followed by a more diverse community of phytoplankton. Stratification was weak after this time.

During stratification, dissolved oxygen levels in the hypolimnion were reduced. In the epilimnion, nitrogen and phosphorus can fall to very low levels during stratification (Reynolds 1976). During the winter, SRP concentrations differed with depth but were similar at all depths during the stratification period. Epilimnetic SRP concentrations decreased during stratification. Nitrogen species concentrations were generally low but increased after the collapse of the cyanobacterial bloom. Surface concentrations of ammonium are often temporarily raised following the breakdown of blooms (McCarthy 1980). Ammonium occurred at the highest concentrations of all the forms of nitrogen measured. *Anabaena* species are



**Fig. 9** Diet composition of juvenile perch (*Perca fluviatilis*) caught in the Lower Karori Reservoir, Wellington, over the 5-month sampling period (2003–04). For each sampling date the diet composition was averaged across all perch caught on that date with food items in their stomachs and that were between 60 and 110 mm total length. Numbers above bars indicate the number of perch.

able to fix atmospheric nitrogen so low levels of nitrogen in the reservoir would not necessarily limit their growth. The *Anabaena* species observed in the Lower Karori Reservoir all formed heterocysts

on occasion during the study period, indicating high likelihood of nitrogen fixation during times of decreased ammonium levels. Both nitrogen and SRP concentrations were at moderate concentrations. pH values were highly variable over time but not depth, with values generally around 7, which is slightly lower than the optimal pH for cyanobacteria growth (Reynolds & Walsby 1975).

There were no observed changes in vertical distribution of plankton populations, though the reason for this may be the lack of persistent stratification. However, the occurrence of thermal stratification was associated with reduced levels of dissolved oxygen in the hypolimnion, high temperatures in the epilimnion ( $>20^{\circ}\text{C}$ , approx. the optimal temperature for cyanobacteria (Robarts & Zohary 1987)), and the development of the cyanobacterial bloom.

### Zooplankton community composition

The bloom of cyanobacteria coincided with a peak of zooplankton abundance, dominated by small crustaceans and rotifers. These are relatively small species that are less vulnerable to predation by visually feeding zooplanktivorous fish such as perch (Hall et al. 1976). Studies elsewhere have shown that fish predation on zooplankton increases during spring and this predation shifts the zooplankton community towards dominance by smaller species (Sommer 1989). However, these smaller species are less effective in controlling phytoplankton blooms because they have lower filtering rates and consume a smaller food size range (Gliwicz 1990). The autumn peak of zooplankton was associated with a slight increase in smaller and more edible phytoplankton taxa and included larger species of zooplankton than the summer peak. Other studies have indicated that the succession of zooplankton from small to large taxa during summer through to autumn is possibly owing to changes in phytoplankton composition paired with a slight reduction in fish predation (Sommer 1989). High densities of filamentous cyanobacteria can also cause a decrease in large species of zooplankton by filtration interference or by the production of inhibitory substances by cyanobacteria species (Burns et al. 1987). Large species, such as *Daphnia* cf. *carinata*, were not abundant, and were at particularly low numbers during summer. *Daphnia* are especially vulnerable to fish predation, which can be high throughout the summer period as this is the time when juvenile fish are most abundant (Gliwicz & Pijanowska 1989).

### Effects of perch predation on the zooplankton community

The structure and abundance of zooplankton communities in New Zealand are traditionally thought to be determined by availability of resources (“bottom-up”) whereas predation (“top-down”) has little influence (Chapman et al. 1975, 1985). This argument is predicated upon observations that New Zealand lakes have few of the invertebrate planktivores that are common in the Northern Hemisphere and obligate planktivorous fish are not widespread (Chapman & Green 1987). However most fish species in New Zealand are zooplanktivorous as juveniles and can occur at extremely high densities (Cryer 1988; Rowe & Chisnall 1996). Introduced zooplanktivorous fish species have the potential to have a significant effect on zooplankton populations that may cascade through the food web to the phytoplankton (Jeppesen et al. 2000).

European perch are known to undergo two dietary shifts during ontogeny (Allen 1935; Craig 1978). Juvenile perch feed on pelagic zooplankton, then shift to benthic invertebrates and, when large enough, feed mainly on fish. However, the diet of perch in this study did not show discrete dietary shifts. Both zooplankton and benthic invertebrates (chironomid larvae) were important dietary components for juvenile perch. Seasonal variation in diet followed the availability of different food sources for perch rather than the dietary switches seen in the Northern Hemisphere. Pelagic zooplankton were a major component of the perch diet, however, large zooplankton taxa were at relatively low densities during the summer when benthic invertebrates became prevalent in the diet. There was no evidence of piscivory in the few large perch caught and most fish had been consuming terrestrial invertebrates. In New Zealand, perch can quickly become very numerous with a small average size (Duncan 1967). Stunted populations are also common in the Northern Hemisphere (Alm 1946). In the Lower Karori Reservoir, the perch population was dominated by perch between 60 and 110 mm total length. Pelagic zooplankton were a large component of the diet of these small fish. Although these small, juvenile perch are not obligate planktivores they could be having a substantial effect on the zooplankton community, which could in turn alter the phytoplankton community via the consumption and excretion of zooplankton.

Thermal stratification and herbivory are known to jointly contribute to the quantity of phytoplankton biomass in freshwater lakes (Mazumder 1994). Stratification and grazing by zooplankton have been

shown to affect phytoplankton succession towards dominance by cyanobacteria (Sterner 1989; Oliver & Ganf 2000). However, the few studies that have been carried out in New Zealand have rejected the hypotheses that predation by fish and grazing by zooplankton affect the structure of phytoplankton communities (e.g., Chapman et al. 1985). Reasons for this conclusion include a lack of planktivorous predators in New Zealand and apparent food limitation of crustacean zooplankton (Chapman & Green 1987). More recent research has suggested that fish may play a role in structuring plankton populations if fish densities are sufficiently high (Jeppesen et al. 1997), and our experimental work using water enclosures within the Lower Karori Reservoir has also provided evidence that perch can significantly alter phytoplankton and zooplankton communities (Smith & Lester 2006). The densities of perch in the reservoir are not known, but the netting survey indicates that the population was dominated by small, juvenile fish. These fish were not exclusively zooplanktivorous but had an opportunistic diet which was dependent on the seasonal availability of prey. However, pelagic zooplankton were a major component of the smaller fishes diet and important larger prey taxa (e.g., *Daphnia* cf. *carinata* and *Ceriodaphnia* cf. *dubia*) were at low abundances in the lake, which suggests strong effects of predation. Although zooplankton communities are generally dominated by small crustaceans and rotifers, the densities of large cladoceran species detected in this study (i.e., >5 individuals litre<sup>-1</sup>) are considered very low (Chapman et al. 1985; Mazumder 1994).

## CONCLUSIONS

The occurrence of cyanobacterial blooms in the Lower Karori Reservoir is probably the result of a number of factors. Inorganic nutrients within the lake were at moderate levels with low concentrations of nitrogen which may favour nitrogen-fixing cyanobacteria over other phytoplankton. Predation pressure by perch (*Perca fluviatilis*) possibly keeps large herbivorous zooplankton at low levels. The phytoplankton community was dominated by large phytoplankton taxa (i.e., species larger than 30 µm) that are probably outside the grazing capacity of most zooplankton. Stratification during the summer months favours buoyant *Anabaena* spp. and mixing helps to elevate nutrient levels in surface waters. Experimental manipulations of these factors, such as nutrient levels or perch abundance, are required

to specifically test for the mechanisms that cause the cyanobacterial blooms and may help determine the relative importance of top-down and bottom-up effects in the Lower Karori Reservoir (see Smith & Lester 2006).

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