Trophic Interactions Promoting Dominance by Cyanobacteria in a Freshwater Pelagic Food Web

Kirsty Fiona Smith

A thesis submitted to Victoria University of Wellington
in fulfillment of the requirements for the degree of
Master of Science in Ecology and Biodiversity

2005

ABSTRACT

Cyanobacterial blooms have occurred in the Lower Karori Reservoir (Wellington) for approximately the last eight years. The dominant species in the past have been identified as *Anabaena lemmermannii* and *A. circinalis*. The reservoir was built in 1874 as part of the first water supply scheme for Wellington City and has been closed to the public since 1906. The catchment was created into a “predator-free” native wildlife sanctuary in 1999. The first severe bloom in the Lower Karori Reservoir occurred during the summer of 2000/01. The objectives of this study were:

- To establish a baseline knowledge of the food web within the Lower Karori Reservoir.
- To follow the chemical and biological dynamics of the Lower Karori Reservoir for an extended period of time to observe seasonal changes associated with the cyanobacterial blooms.
- To experimentally manipulate the trophic levels of the food web to determine which factors (i.e. resources or consumers) were most significant in promoting the growth of cyanobacteria.

I sampled temperature, dissolved oxygen, nutrient levels, and phytoplankton and zooplankton communities from 7 October 2003 to 7 July 2004. I also monitored the diet of the zooplanktivorous fish (perch, *Perca fluviatilis*) present in the lake. The dominant cyanobacteria species was found to be *A. lemmermannii*. Three other cyanobacteria species were present during the study at low abundances, including *A. planktonica* which had not been previously recorded in the reservoir. The bloom of cyanobacteria was associated with thermal stratification. Nutrient concentrations were at moderate levels, characteristic of mesotrophic lakes. The perch population consisted mostly of small-sized individuals that feed predominately on large species of zooplankton that were at low abundances within the lake.

During March 2004, I conducted a food web manipulation experiment within the Lower Karori Reservoir. I sought to test the role of nutrient resources (bottom-up) versus cascading effects of zooplanktivorous perch (*Perca fluviatilis*) (top-down) in controlling cyanobacteria in this lake. Experimental treatments with perch had higher levels of cyanobacterial densities, lower zooplankton species diversity and zooplankton species were generally smaller-sized than in treatments without perch. Nutrient treatments were not favourable for cyanobacteria as the addition of nitrogen probably

meant that nitrogen fixing *Anabaena* species lost competitive advantage over other phytoplankton taxa. It is not known by which mechanism perch promoted cyanobacterial growth since this was not directly measured. Plankton community composition was altered by all treatments.

This study indicates that blooms of *Anabaena* species in the Lower Karori Reservoir are the result of a number of complex interactions within the lake food web. Low nitrogen levels favour dominance by the nitrogen fixing cyanobacteria, which bloom during thermal stratification as they are able to maintain their position in the water column due to buoyancy control. Predation pressure by perch is likely keeping large filter-feeding zooplankton at low levels and thus reducing grazing pressure on phytoplankton. Phosphorus excretion by perch also probably favours cyanobacteria.

An eradication of perch within the Lower Karori Reservoir would probably contribute to prevent cyanobacteria predominance. The removal of perch from the reservoir should be reasonably simple due its small size and contained area. Other methods which may help reduce cyanobacterial blooms within the reservoir include artificial mixing to prevent stratification. However, these methods can be expensive to install and run.

ACKNOWLEDGEMENTS

This study would never have been completed without the help and support of a great many people. Firstly, I would like to thank my supervisor Dr. Phil Lester for all his advice, support and encouragement. Also, for always being available for assistance when things got tough especially once I moved away from Wellington. I thank Victoria University and the Harris Memorial Trust for financial support during my study. I would like to acknowledge the following individuals for their invaluable support and assistance with this study:

- A special acknowledgement must go to all my field assistants who come out and helped me during a very wet and windy summer. Thank you Vivian Dalley, Annita Patel, Daniel Hawke, Myregel Carambas, Hayley Campbell, Sarah Verry and Gitika Mangar. An especially big thank you to Brad McNeil and Davina Rowan – my number one helpers!
- Thank you to Cecile Stephens, Adrian Pike and Daniel Hawke for assistance in building the enclosures and also Adrian for helping get them out again!
- Susie Wood for advice, encouragement and help with plankton identification.
- All the staff at the Karori Wildlife Sanctuary especially Keith Kalder, Raewyn Empson and the op shed staff.
- The technicians at the School of Biological Sciences especially Peter Watson for supplying sedimentation chambers and other lab equipment, Lesley Milicich for supplying chemicals and sampling bottles, and Jo Long for the aquarium equipment.
- Shirley Pledger (VUW) for statistical advice.
- Bob Wear (VUW) for help with perch stomach content analyses, and sampling equipment.
- Ken Ryan (VUW) for advice and help with chlorophyll *a* analyses.
- George Gibbs (VUW) for advice and assistance with invertebrate identification.
- Lindsay Chadderton (DOC) for supplying the gill nets.
- To the SBS ‘Bug Group’, my parents Roy and Jan Smith, and Suzanne Duncan for their support and for reviewing my work.
- A special thanks to Daniel Hawke for all his support and encouragement (even from long distances!).

TABLE OF CONTENTS

1. THESIS INTRODUCTION.....	1
1.1 Thermal stratification.....	2
1.2 Bottom-up versus top-down control.....	3
1.3 The Karori Wildlife Sanctuary.....	5
1.4 Aims and outline of this study.....	7
1.5 REFERENCES.....	8
 2. Whole lake monitoring to determine the chemical and biological interactions of the Lower Karori Reservoir (Wellington).....	 15
2.1 Abstract.....	15
2.2 Keywords.....	15
2.3 INTRODUCTION.....	16
2.3.1 Thermal stratification.....	16
2.3.2 Cyanobacteria dominance.....	17
2.3.3 The Lower Karori Reservoir.....	18
2.4 MATERIALS AND METHODS.....	19
2.4.1 Field methods.....	19
2.4.2 Laboratory methods.....	20
2.4.3 Statistical analyses.....	20
2.5 RESULTS.....	21
2.5.1 Physical and chemical dynamics.....	21
2.5.2 Phytoplankton and zooplankton communities.....	26
2.5.3 Perch size structure and diet.....	30
2.6 DISCUSSION.....	33
2.6.1 Effects of thermal stratification on the phytoplankton community and chemical dynamics.....	33
2.6.2 Zooplankton community composition.....	34

2.6.3 The role of perch predation in structuring the zooplankton community and possible top-down effects on phytoplankton.....	35
2.7 CONCLUSIONS.....	37
2.8 REFERENCES.....	37
3. Cyanobacterial blooms appear to be driven by top-down rather than bottom-up effects in the Lower Karori Reservoir (Wellington).....	43
3.1 Abstract.....	43
3.2 Keywords.....	43
3.3 INTRODUCTION.....	44
3.4 MATERIALS AND METHDOS.....	45
3.4.1 Study site.....	45
3.4.2 Experimental design and field methods.....	46
3.4.3 Laboratory methods.....	48
3.4.4 Statistical analyses.....	49
3.5 RESULTS.....	50
3.6 DISCUSSION.....	58
3.7 REFERENCES.....	61
4. GENERAL DISCUSSION.....	66
4.1 Whole lake monitoring.....	66
4.2 Food web manipulation.....	67
4.3 The success of biomanipulation.....	68
4.4 Conclusions.....	69
4.5 Future directions.....	70
4.6 REFERENCES.....	71

LIST OF TABLES

Table 2.1	Results of a repeated measures ANOVA on $\log(x + 1)$ transformed data to determine the effects of depth and time on plankton abundance, nutrient concentrations and pH levels.....	25
Table 2.2	Plankton taxa recorded in the Lower Karori Reservoir during the 9-month sampling period. Taxa are listed in order of abundance over the entire monitoring period.....	25
Table 3.1	Results of a repeated measures ANOVA on $\log(x + 1)$ transformed data to determine the effects of nutrient and fish additions on phytoplankton and zooplankton populations.....	54
Table 3.2	Pairwise Test comparisons for analysis of similarities (ANOSIM) on $\log(x + 1)$ transformed data.....	57

LIST OF FIGURES

Fig. 2.1	Temperature ($^{\circ}\text{C}$) depth profiles for the Lower Karori Reservoir over the 9-month period showing the onset of stratification during the summer period.....	22
Fig. 2.2	Dissolved oxygen (mg L^{-1}) depth profiles for the Lower Karori Reservoir over the 9-month period showing reduced oxygen levels at depth during the summer months.....	23
Fig. 2.3	Average (a) total nitrogen, (b) dissolved phosphorus levels (mg L^{-1}), (c) pH, and (d) Secchi disc depth (m) (± 1 standard error) for the 9-month sampling period.....	24
Fig. 2.4	Average total phytoplankton (cells ml^{-1}) and total zooplankton (litre^{-1}) counts (± 1 standard error) for the 9-month period.....	28
Fig 2.5	Average cyanobacteria (cells ml^{-1}) counts (± 1 standard error) for the 9-month sampling period averaged across all depths.....	28
Fig. 2.6	Seasonal changes in abundance of (a) phytoplankton and (b) zooplankton groupings, as represented as a proportion of total phytoplankton and zooplankton abundance respectively.....	29
Fig. 2.7	Non-metric multidimensional scaling (MDS, using Bray-Curtis dissimilarity) on $\log(x + 1)$ transformed data of relative species composition during periods of thermal stratification and complete water column mixing	29

Fig. 2.8	Size and diet of perch (<i>Perca fluviatilis</i>) in the Lower Karori Reservoir. (a) Length distribution of all perch caught in the Karori Reservoir during the 5 month sampling period and (b) Proportion of zooplankton in the stomach contents in relation to size of the perch	31
Fig. 2.9	Diet composition of perch caught in the Lower Karori Reservoir during the 5 month sampling period.....	32
Fig. 3.1	Plastic enclosures used in the food web field manipulation experiment.....	46
Fig. 3.2	Mean (a) total nitrogen and (b) dissolved phosphorus (mg L^{-1}) (± 1 standard error) under each treatment.....	47
Fig. 3.3	Mean cyanobacteria (cells ml^{-1}) levels (± 1 standard error) under each treatment.....	53
Fig. 3.4	Grand mean values over experiment duration (± 1 standard error). (a) Cyanobacteria (cells ml^{-1}), (b) Total phytoplankton (cells ml^{-1}), (c) Chlorophyll <i>a</i> ($\mu \text{ litre}^{-1}$), (d) Edible phytoplankton (cells ml^{-1}), (e) Phytoplankton species diversity (H' , Shannon-Weiner diversity index), and (f) Secchi disc depth (m).....	55
Fig. 3.5	Grand mean values over experiment duration (± 1 standard error). (a) Total zooplankton (litre^{-1}), (b) Large zooplankton (litre^{-1}), and (c) Zooplankton species diversity (H' , Shannon-Weiner diversity index).....	56
Fig. 3.6	Non-metric multidimensional scaling (MDS, Bray-Curtis dissimilarity) on $\log(x + 1)$ transformed data of relative species composition of the eight experimental enclosures.....	57

1. THESIS INTRODUCTION

The composition of phytoplankton communities is the result of a number of complex interactions among various physical, chemical, and biological environmental factors (Reynolds 1989). In some temperate lakes a shift in phytoplankton community structure from eukaryotic species to prokaryotic cyanobacteria may occur during summer. Cyanobacteria most commonly become dominant during periods of thermal stratification and are often limited to this period (Viner & White 1987). Dominance by cyanobacteria can be attributed to many factors, including the ability of some species to fix atmospheric nitrogen and thus utilise low nitrogen to phosphorous ratios (Smith 1983), buoyancy regulation (Reynolds et al. 1987), and relatively reduced zooplankton grazing (de Bernardi & Giussani 1990).

Blooms of cyanobacteria decrease the economic and recreational values of freshwater bodies and in some cases are potentially harmful to humans and wildlife (Oliver & Ganf 2000). Animal poisonings by toxic cyanobacteria in New Zealand were first published by Flint (1966). Cyanobacteria blooms have since been frequently recorded around New Zealand (Pridmore & Etheredge 1987). The most common bloom-forming genera in New Zealand lakes are *Anabaena*, *Microcystis*, and *Cylindrospermopsis* (Wood 2005). These genera are also known to form blooms overseas (Chorus & Bartram 1999; Haider et al. 2003). Wood (2005), in a recent survey of the distribution and species composition of bloom forming-cyanobacteria in New Zealand, noted that the occurrence of cyanobacterial blooms in freshwater lakes had increased since 1987 (Pridmore & Etheredge 1987). However, this increase may have been due to more intensive and extensive sampling (Wood 2005). Interestingly, her survey indicated that cyanobacteria species composition in New Zealand has changed in the last 15-30 years. Wood (2005) identified six new bloom forming cyanobacteria species and three species were already known to occur in New Zealand lakes but had not previously been recorded as forming blooms.

There has been a long history of debate over to what extent phytoplankton communities in freshwater lakes are controlled by resources [bottom-up control, *sensu* McQueen et al. (1986); that is phytoplankton are regulated by light, nutrients etc.] or by predation (top-down control).

Traditionally, ecosystems have been considered to be controlled by resource quantity and quality (e.g. White 1978). Nutrients do affect phytoplankton community composition. Changes in nutrient concentrations that correspond to changes in species composition support the importance of bottom-up control (Tilman et al. 1982). However, phytoplankton communities are not only dependent on resource levels, as grazing by herbivorous zooplankton can also structure phytoplankton communities (Sterner 1989). Evidence for consumer control of phytoplankton has generated theories such as the trophic cascade model (Carpenter & Kitchell 1993; Carpenter et al. 1985) and trophic “biomanipulation” (Shapiro & Wright 1984; Shapiro et al. 1975)

1.1 Thermal stratification

Thermal stratification affects the physical, chemical and biological interactions of a lake. When a lake becomes stratified the water column becomes separated into three layers. The upper layer (the epilimnion) is warm and well mixed. It lies above the metalimnion (or thermocline) which is a region of rapid decreases in temperature. The bottom layer, hypolimnion, is colder and usually dark (Jolly & Irwin 1975). In temperate lakes, thermal stratification can affect phytoplankton seasonal succession by changing the relative sedimentation rates of certain taxa (Reynolds 1984). When lakes stratify, large heavy organisms, in particular diatoms, settle out of the water column more rapidly than in a homothermous lake. The phytoplankton community then shifts to become dominated by small organisms with relatively high growth rates or those with buoyancy regulation (Proulx et al. 1996). Massive populations of cyanobacteria can accumulate in the epilimnion because of their capacity for positive buoyancy. Nitrogen fixing species, such as *Anabaena* spp., have an advantage in New Zealand lakes, which are characteristically lacking in nitrogen (Viner & White 1987). They are most abundant during stratification, where there would otherwise be a decrease in production due to reduced nutrient concentrations during stratification (Viner & White 1987). The ability of cyanobacteria to control their vertical distribution under conditions of stable stratification, especially in relation to nutrient availability, may be crucial in determining the succession of phytoplankton towards dominance by cyanobacteria. Stable stratification and declining nutrient availability are the two key environmental variables stimulating phytoplankton succession (Reynolds 1984) and often lead to cyanobacterial blooms in temperate lakes.

1.2 Bottom-up versus top-down control

Minimizing nutrient inputs into lakes is a popular management tool for lakes that experience cyanobacterial blooms (Carpenter & Lathrop 1999). Reducing phosphorus and nitrogen levels follows on from the assumption that phytoplankton biomass is primarily controlled by “bottom-up” factors. Nutrient reductions can often have limited success, since large reserves of nutrients can be released from the bottom sediments and improvements in water quality can take several years (Shapiro et al. 1975). An alternative approach for the control of cyanobacterial blooms is to manipulate the lake ecosystem to increase the consumption of phytoplankton by zooplankton. This “top-down” model predicts that each level in a food web is inversely and directly related to the trophic levels above and below it (Carpenter et al. 1985). By decreasing the abundance of zooplanktivorous fish, the abundance of large herbivorous zooplankton should increase, and phytoplankton biomass should decrease due to more intensive grazing by these herbivores (Brett & Goldman 1996). This manipulation of the food web was termed “biomanipulation” and was proposed for lakes where nutrient input is fixed or could not be significantly reduced (Shapiro et al. 1975). It has been well documented that the removal or reduction of zooplanktivorous fish can cause an increase in large filter feeding zooplankton and consequently a decrease in phytoplankton biomass, or where the addition of zooplanktivorous fish is associated with an increase in phytoplankton biomass (Brooks & Dodson 1965; Carpenter & Kitchell 1993; Hall et al. 1976; Sarnelle 1992; Zaret & Paine 1973). Manipulation of the food web to promote zooplankton abundance has been widely used as a lake management tool to control phytoplankton blooms (e.g. Shapiro & Wright 1984).

These two perspectives on food webs have differing predictions about how the biomass of different trophic levels is controlled. The nutrient loading model assumes the ecosystems are regulated from the “bottom-up” (White 1978). This model hypothesizes two outcomes. One, that the more productive an ecosystem, the more trophic levels it will support (Oksanen et al. 1981), and two, that the higher the primary production the higher the biomass at all trophic levels (McQueen et al. 1986). The alternative “top-down” approach states that the top predator in a system regulates the biomass of lower trophic levels (Pace et al. 1999). Some models incorporate both theories. McQueen et al. (1986) predicted that bottom-up control is stronger at the base of

the food web and top-down control is stronger at the higher levels. Consequently, zooplanktivorous fish have a greater effect on zooplankton than nutrients do and phytoplankton biomass would be principally controlled by nutrient availability and to a lesser extent by higher trophic levels.

A recent meta-analysis of the aquatic trophic cascade literature showed that experimental treatments with planktivorous fish did generally result in decreased herbivore abundance and increased primary producer biomass compared to treatments without fish (Brett & Goldman 1996). However, phytoplankton biomass response to the fish treatments was highly variable with very strong responses in about one third of the cases and weak responses in the others. A second analysis by the same authors provided strong support for the model described by McQueen et al. (1986), where zooplanktivorous fish have a strong impact on zooplankton biomass but phytoplankton biomass is more strongly controlled by nutrient availability than by top-down effects (Brett & Goldman 1997). These results suggest that under certain conditions increased primary production by nutrient additions may not be efficiently transferred to herbivorous zooplankton biomass. The authors felt that these results were because the “phytoplankton stimulated by these treatments may have been difficult to ingest, digest, or were nutritionally inadequate, or a combination of these factors” (Brett & Goldman 1997). This problem of “inedible” algae is significant and it has been shown that phytoplankton may be resistant to grazing for many reasons including size, shape, or taxonomic group (Bell 2002; Bergquist & Carpenter 1986; Gliwicz 1990; Porter 1977; Webster & Peters 1978). One important assumption of the trophic cascade theory is that systems can only exhibit trophic cascades if the dominant primary producers are edible species (Agrawal 1998; Strong 1992). If inedible species are present, edible species are vulnerable to grazing loss and inedible species have an advantage due to reduced competition and access to nutrients released in the process of zooplankton digestion (Bell 2002; Bohannan & Lenski 1999; Gliwicz 1990; Sterner 1986).

The size distribution of filter-feeding herbivores also determines the susceptibility of the phytoplankton community to grazing. It is well known that large-bodied zooplankton can consume larger phytoplankton (Burns 1968; Hall et al. 1976) and phytoplankton larger than 30 μm are for the most part inedible (McCauley & Downing 1985). Large zooplankton, particularly

cladocerans from the genus *Daphnia* (Leibold 1989), will be more effective in controlling algal blooms. These species, however, are more vulnerable to predation by planktivorous fish (Brooks & Dodson 1965) and would be the first to benefit from reduced fish predation. The promotion of large-bodied zooplankton and the probability of inedible phytoplankton blooms developing are the primary factors for the success of food web manipulations in freshwater ecosystems (McQueen 1990).

Predation on zooplankton communities in New Zealand has previously been thought to have little impact on the size and abundance of zooplankton communities. Bottom-up hypotheses are more commonly induced to explain the structure of zooplankton communities (Chapman et al. 1975; Chapman et al. 1985). Reasons for this result include a generally low fecundity of crustacean zooplankton (Chapman et al. 1985) and that zooplankton clutch size has been found to be related to phytoplankton biomass (e.g. Burns 1992). New Zealand lakes are also lacking in obligate planktivorous fish and invertebrates that are abundant in the Northern Hemisphere (Chapman & Green 1987). In spite of this evidence, a few authors have suggested that top-down control by fish may be significant in some New Zealand lakes (Cryer 1988; Jeppesen et al. 1997; Jeppesen et al. 2000; Rowe & Chisnall 1996). This suggestion has been based on the fact that juvenile planktivorous fish can occur at extremely high densities, high fish densities have been correlated with low zooplankton biomass, and New Zealand lakes characteristically have a low ratio of zooplankton to phytoplankton biomass that is consistent with high levels of fish predation (Jeppesen et al. 1997; Jeppesen et al. 2000). However, the cascading effects of fish predation to the phytoplankton have been found to be limited as most of the phytoplankton that reach high densities in New Zealand lakes are generally large celled and may not be easily grazed by zooplankton (Burns 1998; Malthus & Mitchell 1990).

1.3 The Karori Wildlife Sanctuary

The Karori Wildlife Sanctuary is situated around the two Karori Reservoirs in Wellington. The sanctuary encompasses 252 hectares and includes a mixture of shrub and hardwood regenerating forest (Lynch 1995). The Lower Karori Reservoir is a warm monomictic lake with a mean depth of 8.2 m and a maximum depth of over 20 m. The Lower Karori Reservoir was completed in 1874 as part of the first water supply scheme for Wellington City. Farming continued in the

catchment until 1906, when all stock were removed (Burch 1997). The area was then closed to the public.

Cyanobacterial blooms caused by *Anabaena* species have occurred in the Lower Karori Reservoir for about the last 8 years (Wood 2005). The blooms have a number of associated detrimental effects on the Sanctuary including visual degradation, odor problems, possible health risks to humans and wildlife, and have been associated with fish deaths in the past (Wood 2005).

The surrounding catchment has been developed into a wildlife sanctuary after the reservoir ceased to be used as a water supply. An 8.6 km predator-proof fence surrounding the catchment was completed in 1999 and a multi-species eradication programme was completed in 2000. This pest management programme is on-going. Two species of exotic fish still remain in the Lower Karori Reservoir: brown trout (*Salmo trutta*) and European perch (*Perca fluviatilis*). In 1878 perch were released into the Lower Karori Reservoir by the Wellington Acclimatisation Society (Thomson 1922). Perch naturally occur in still or slow-flowing temperate waters and are native to the Northern Hemisphere (McDowall 1990). In New Zealand they are found in many lake and river systems throughout both islands. Despite being introduced as a game fish, perch is not widely fished for. This is generally because despite the potential for attaining large size (up to 3 kg) (Jellyman 1980), perch populations in New Zealand are characterized by large populations with small sized fish (Duncan 1967). The main reason for this stunted size distribution is probably that perch have very few natural predators in New Zealand such as the large predatory fishes that are present in the Northern Hemisphere (e.g. European pike) (Jellyman 1982; McDowall 1990). Perch can be an important food source for shags (*Phalacrocorax* spp.) and other piscivorous birds (McDowall 1987). Duncan (1967) also hypothesized that because of a large amount of suitable spawning habitat available in some waters; reproduction can be very high, leading to severe intraspecific competition. Under high intraspecific competition perch are well known to form stunted populations (Alm 1946). This competition between age classes results in low individual growth rate and so the population tends towards small individuals (Persson 1988).

Perch spawn in spring and potentially undergo two diet shifts during their ontogeny (Allen 1935; Craig 1978). Perch have been found to feed in sequence on three types of food. Juvenile perch feed on pelagic zooplankton, then shift to benthic invertebrates and when large enough, feed mainly on fish (Allen 1935). These diet switches are therefore associated with a change from the pelagic zone to benthic habitat (Persson 1986) and may suggest that the diet shift is relatively discrete. Perch are usually abundant, with slow growth and are dominated by strong year classes (Deelder 1951). The dominant cohorts are found to suppress subsequent year-classes in lakes where perch are the top predatory fish (Treasurer 1993). In such systems, perch populations often have large oscillations as the result of cannibalistic and competitive interactions. Populations will switch between being dominated by large numbers of adult fish, which will prevent recruitment through cannibalism, and having high numbers of juveniles with only a few adults present (Claessen et al. 2000; Persson et al. 2000; Wahlstrom et al. 2000).

1.4 Aims and outline of this study

This study aimed to determine the role of bottom-up versus cascading top-down effects in controlling cyanobacteria growth in the Lower Karori Reservoir. I investigated how thermal stratification influenced the physical and chemical interactions in the lake and how these changes in resources shaped the phytoplankton community structure. The diet of the perch population and how predation by perch affected herbivorous zooplankton size and abundance was also studied. The associated changes in zooplankton abundance were monitored. Regular lake sampling was carried out for a 9-month period from 7 October 2003 to 7 July 2004. Perch populations were sampled regularly between 23 December 2003 and 4 May 2004. A manipulative field experiment was conducted in March 2004 for a 4-week period. This survey and experiment was designed to provide some base knowledge of the food web dynamics in the Lower Karori Reservoir. It may also help form the basis of a potential management plan for the regulation of cyanobacterial blooms by the Karori Wildlife Sanctuary.

This thesis is structured into four chapters, beginning with this introduction. Chapter Two presents the results of the 9-month whole lake sampling programme, in which water column dynamics, nutrient concentrations, plankton communities and the perch population were monitored. Chapter Three describes the food web manipulation experiment that was conducted

within plastic enclosures situated in the lake, in an attempt to experimentally quantify the effects of perch and nutrients on cyanobacteria abundance. The responses of the plankton populations to addition of juvenile perch and the addition of nutrients are described. The general conclusions of this study are presented in Chapter Four. Chapters Two and Three are written in the format of scientific papers each with separate abstracts, methods, results, discussions and references. Because of this style there is some repetition in the introduction and methods sections.

1.5 REFERENCES

- Agrawal, A. A. 1998: Algal defense, grazers, and their interactions in aquatic trophic cascades. *Acta Oecologica* 19: 331-337.
- Allen, K. R. 1935: The food and migration of the perch (*Perca fluviatilis*) in Windermere. *Journal of Animal Ecology* 4: 264-273.
- Alm, G. 1946: Reasons for the occurrence of stunted fish populations with special regard to perch. *Report from the Swedish State Institute of Freshwater Research, Drottningholm* 25.
- Bell, T. 2002: The ecological consequences of unpalatable prey: phytoplankton response to nutrient and predator additions. *Oikos* 99: 59-68.
- Bergquist, A. M.; Carpenter, S. R. 1986: Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67: 1351-1360.
- Bohannon, B. J. M.; Lenski, R. E. 1999: Effect of prey heterogeneity on the response of a model food chain to resource enrichment. *The American Naturalist* 153: 73-82.
- Brett, M. T.; Goldman, C. R. 1996: A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Sciences of the United States of America* 93: 7723-7726.
- Brett, M. T.; Goldman, C. R. 1997: Consumer versus resource control in freshwater pelagic food webs. *Science* 275: 384-386.
- Brooks, J. L.; Dodson, S. I. 1965: Predation, body size and composition of plankton. *Science* 150: 28-35.
- Burch, J. 1997: The Karori reservoir area: a brief history. Wellington, New Zealand, Karori Historical Society. 40 p.

- Burns, C. W. 1968: The relationship between body size of filter feeding cladocera and the maximum size of particle ingested. *Limnology and Oceanography* 13: 675-678.
- Burns, C. W. 1992: Population dynamics of crustacean zooplankton in a mesotrophic lake, with emphasis on *Boeckella hamata* Brehm (Copepoda:Calanoida). *Internationale Revue der gesamten Hydrobiologie* 77: 553-577.
- Burns, C. W. 1998: Planktonic interactions with an austral bias: implications for biomanipulation. *Lakes and Reservoirs: Research and Management* 3: 95-104.
- Carpenter, S. R.; Lathrop, R. C. 1999: Lake restoration: capabilities and needs. *Hydrobiologia* 395/396: 19-28.
- Carpenter, S. R.; Kitchell, J. F. 1993: The trophic cascade in lakes. Cambridge, Cambridge University Press. 385 p.
- Carpenter, S. R.; Kitchell, J. F.; Hodgson, J. R. 1985: Cascading trophic interactions and lake productivity. *BioScience* 35: 634-639.
- Chapman, M. A.; Green, J. D. 1987: Zooplankton ecology. In: Viner, A. B. ed. Inland waters of New Zealand. Wellington, New Zealand, DSIR Bulletin 241. Pp. 225-263.
- Chapman, M. A.; Green, J. D.; Jolly, V. H. 1975: Zooplankton. In: Jolly, V. H.; Brown, J. M. A. eds. New Zealand lakes. Auckland, Auckland University Press. Pp. 211-230.
- Chapman, M. A.; Green, J. D.; Jolly, V. H. 1985: Relationships between zooplankton abundance and trophic state in seven New Zealand lakes. *Hydrobiologia* 123: 119-136.
- Chorus, I.; Bartram, J. 1999: Toxic cyanobacteria in water: a guide to their public health consequences, monitoring and management. London, E&FN Spon. 416 p.
- Claessen, D.; de Roos, A. M.; Persson, L. 2000: Dwarfs and giants: cannibalism and competition in size-structured populations. *The American Naturalist* 155: 219-237.
- Craig, J. F. 1978: A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshwater Biology* 8: 59-68.

- Cryer, M. 1988: Predatory impact of New Zealand smelt on natural populations of zooplankton. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 23: 1778-1783.
- de Bernardi, R.; Giussani, G. 1990: Are blue-green algae a suitable food for zooplankton? An overview. *Hydrobiologia* 200/201: 29-41.
- Deelder, C. L. 1951: A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. *Hydrobiologia* 3: 357-378.
- Duncan, K. W. 1967: The food and population structure of perch (*Perca fluviatilis* L.) in Lake Mahinerangi. *Transactions of the Royal Society of New Zealand, Zoology* 9: 45-52.
- Flint, E. A. 1966: Toxic algae in some New Zealand freshwater ponds. *New Zealand Veterinary Journal* 14: 181-185.
- Gliwicz, Z. M. 1990: Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 83-97.
- Haider, S.; Naithani, V.; Viswanathan, P. N.; Kakkar, P. 2003: Cyanobacterial toxins: a growing environmental concern. *Chemosphere* 52: 1-21.
- Hall, D. J.; Threlkeld, S. T.; Burns, C. W.; Crowley, P. H. 1976: The size-efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* 7: 177-208.
- Jellyman, D. J. 1980: Age, growth, and reproduction of perch, *Perca fluviatilis* L., in Lake Pounui. *New Zealand Journal of Marine and Freshwater Research* 14: 391-400.
- Jellyman, D. J. 1982: Research on perch. *Freshwater Catch Summer 1982*: 19-20.
- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Burns, C. W. 1997: Do planktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand Journal of Marine and Freshwater Research* 31: 163-173.
- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Christoffersen, K.; Burns, C. W. 2000: Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research* 22: 951-968.

- Jolly, V. H.; Irwin, J. 1975: Thermal conditions. *In*: Jolly, V. H.; Brown, J. M. A. *eds*. New Zealand lakes. Auckland, Auckland University Press. Pp. 90-105.
- Leibold, M. A. 1989: Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist* 134: 922-949.
- Lynch, J. 1995: Back to the future: Karori - from reservoir to wildlife sanctuary. *Forest and Bird* 12-19.
- Malthus, T.; Mitchell, S. F. 1990: On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. *Freshwater Biology* 22: 383-394.
- McCauley, E.; Downing, J. A. 1985: The prediction of cladoceran grazing rate spectra. *Limnology and Oceanography* 30: 202-212.
- McDowall, R. M. 1987: Impacts of exotic fishes on the native fauna. *In*: Viner, A. B. *ed*. Inland waters of New Zealand. Wellington, New Zealand, DSIR Bulletin. Pp. 333-347.
- McDowall, R. M. 1990: New Zealand freshwater fishes: a natural history and guide. Heinemann Reed. MAF Publication Group. 553 p.
- McQueen, D. J. 1990: Manipulating lake community structure: where do we go from here? *Freshwater Biology* 23: 613-620.
- McQueen, D. J.; Post, J. R.; Mills, E. L. 1986: Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1571-1581.
- Oksanen, L.; Fretwell, S. D.; Arruna, J.; Niemela, P. 1981: Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118: 240-261.
- Oliver, R. L.; Ganf, G. G. 2000: Freshwater blooms. *In*: Whitton, B. A.; Potts, M. *eds*. The ecology of cyanobacteria. Kluwer Academic Publishers. Pp. 149-194.
- Pace, M. L.; Cole, J. J.; Carpenter, S. R.; Kitchell, J. F. 1999: Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14: 483-488.
- Persson, L. 1986: Effects of reduced interspecific competition on resource utilization in perch (*Perca fluviatilis*). *Ecology* 67: 355-364.

- Persson, L. 1988: Asymmetries in competitive and predatory interactions in fish populations. *In*: Ebenman, B.; Persson, L. eds. *Size-Structured Populations: Ecology and Evolution*. Springer-Verlag. Pp. 203-218.
- Persson, L.; Bystrom, P.; Wahlstrom, E. 2000: Cannibalism and competition in Eurasian perch: population dynamics of an ontogenetic omnivore. *Ecology* 81: 1058-1071.
- Porter, K. G. 1977: The plant-animal interface in freshwater ecosystems. *American Scientist* 65: 159-170.
- Pridmore, R. D.; Etheredge, M. K. 1987: Planktonic cyanobacteria in New Zealand inland waters: distribution and population dynamics. *New Zealand Journal of Marine and Freshwater Research* 21: 491-502.
- Proulx, M.; Pick, F. R.; Mazumder, A.; Hamilton, P. B.; Lean, D. R. S. 1996: Effects of nutrients and planktivorous fish on the phytoplankton of shallow and deep aquatic systems. *Ecology* 77: 1556-1572.
- Reynolds, C. S. 1984: *The ecology of freshwater phytoplankton*. Cambridge, Cambridge University Press. 384 p.
- Reynolds, C. S. 1989: Physical determinants of phytoplankton succession. *In*: Sommer, U. ed. *Plankton ecology: succession in plankton communities*. Berlin, Springer-Verlag. Pp. 9-56.
- Reynolds, C. S.; Oliver, R. L.; Walsby, A. E. 1987: Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *New Zealand Journal of Marine and Freshwater Research* 21: 379-390.
- Rowe, D. K.; Chisnall, B. L. 1996: Size-related differences in diel feeding activity, prey selection and nocturnal migration strategy for the planktonic larvae of *Gobiomorphus cotidianus* in Lake Rotiti (NI), New Zealand. *Archiv für Hydrobiologie* 135: 485-497.
- Sarnelle, O. 1992: Nutrient enrichment and grazer effects on phytoplankton in lakes. *Ecology* 73: 551-560.
- Shapiro, J.; Wright, D. I. 1984: Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. *Freshwater Biology* 14: 371-383.

- Shapiro, J.; Lamarra, V.; Lynch, M. 1975: Biomanipulation: an ecosystem approach to lake restoration. *In: Brezonik, P. L.; Fox, J. L. eds. Water quality management through biological control.* Gainesville, University of Florida. Pp. 85-96.
- Smith, V. H. 1983: Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671.
- Sterner, R. W. 1986: Herbivores direct and indirect effects on algal populations. *Science* 231: 605-607.
- Sterner, R. W. 1989: The role of grazers in phytoplankton succession. *In: Sommer, U. ed. Plankton ecology: succession in plankton communities.* Berlin, Springer Verlag. Pp. 107-170.
- Strong, D. R. 1992: Are trophic cascades all wet? Differentiation and donor control in speciose ecosystems. *Ecology* 73: 747-754.
- Thomson, G. M. 1922: The naturalisation of animals and plants in New Zealand. London, Cambridge University Press. 607 p.
- Tilman, D.; Kilham, S. S.; Kilham, P. 1982: Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics* 13: 49-72.
- Treasurer, J. 1993: The population biology of perch, *Perca fluviatilis* L., in simple fish communities with no top piscivore. *Ecology of Freshwater Fish* 2: 16-22.
- Viner, A. B.; White, E. 1987: Phytoplankton growth. *In: Viner, A. B. ed. Inland waters of New Zealand.* Wellington, New Zealand, DSIR Bulletin 241. Pp. 191-223.
- Wahlstrom, E.; Persson, L.; Diehl, S.; Bystrom, P. 2000: Size-dependent foraging efficiency, cannibalism and zooplankton community structure. *Oecologia* 123: 138-148.
- Webster, K.; Peters, R. H. 1978: Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnology and Oceanography* 23: 1238-1245.
- White, T. C. R. 1978: The importance of a relative shortage of food in animal ecology. *Oecologia* 33: 71-86.
- Wood, S. A. 2005: Bloom forming and toxic cyanobacteria in New Zealand: species diversity, distribution, cyanotoxin production and accumulation of microcystins in selected freshwater

organisms. Unpublished PhD thesis, Victoria University and Massey University, Wellington, New Zealand. 306 p.

Zaret, T. M.; Paine, R. T. 1973: Species introduction in a tropical lake. *Science* 182: 449-455.

2. Whole lake monitoring to determine the chemical and biological interactions of the Lower Karori Reservoir (Wellington)

2.1 Abstract Blooms of *Anabaena* species have occurred in the Lower Karori Reservoir (Wellington) for approximately the last eight years. The aims of this part of the study were to determine how thermal stratification influences the chemical dynamics in the reservoir and to monitor seasonal changes in the plankton community associated with a cyanobacterial bloom. The diet and size classes of the perch population were also examined. Thermal stratification caused the hypolimnion to become anoxic but did not affect nutrient depth distributions. Nutrient levels were at moderate concentrations that are characteristic of mesotrophic lakes. Dissolved phosphorus concentrations were reduced during stratification and total nitrogen levels became elevated after the breakdown of the bloom. A bloom of *Anabaena lemmermannii* occurred with the onset of thermal stratification. Zooplankton abundance also peaked during stratification and consisted mainly of rotifers. The perch caught during this study were typically small-sized individuals that diet studies showed to consume mostly large-sized zooplankton. The development of cyanobacterial blooms in the Lower Karori Reservoir is probably due to a combination of factors including low nitrogen levels that favour nitrogen-fixing cyanobacteria and the ability of cyanobacteria to control their buoyancy and maintain their position in the water column during thermal stratification. Also, predation by perch is likely to be keeping large zooplankton species at low levels and reducing grazing pressure on phytoplankton populations.

2.2 Keywords Cyanobacteria; *Anabaena*; phytoplankton; zooplankton; thermal stratification; nitrogen; phosphorus; *Perca fluviatilis*; Karori Wildlife Sanctuary

2.3 INTRODUCTION

Blooms of cyanobacteria in freshwater lakes are a principal water quality problem worldwide and have increasingly become more extensively studied due to economic and recreation impacts (e.g. Steffensen et al. 1999). A “bloom” is hard to define but generally the term refers to an increase in phytoplankton biomass that is much higher than the average biomass for the waterbody or to a concentration of phytoplankton cells that commonly causes a nuisance to humans (Oliver & Ganf 2000). For example, concentrations of cyanobacteria cells in excess of 15 000 cells ml⁻¹ are considered a “bloom” in New Zealand recreational waters as this concentration of cells can potentially cause toxicity problems for general recreational activities. Cyanobacteria that form blooms are principally species that have gas vacuoles and can actively maintain their position in the water column to achieve the best possible conditions for nutritional and photosynthetic requirements (Reynolds et al. 1987).

2.3.1 Thermal stratification

The mechanisms by which surface blooms form are not clear-cut, but depend on the co-occurrence of at least three characteristics: a pre-existing cyanobacterial population, a number of organisms with positive buoyancy, and a stable water column (Reynolds 1984). The water column of a lake stabilizes and thermally stratifies in times of reduced wind velocity and increased temperatures. These conditions result in each layer of water having its own characteristics of motion, temperature and density (Reynolds 1984). The epilimnion is the upper layer which is warm, well mixed and aerated by oxygen from the atmosphere. Below this layer is a zone of rapidly decreasing temperature, the metalimnion (or thermocline), and then a deep, colder, and usually dark bottom layer, the hypolimnion (Jolly & Irwin 1975). Stratification can affect chemical and biological interactions within the lake. Stratified lakes often show discontinuities in nutrient concentrations, pH and dissolved oxygen (Reynolds 1976). Phytoplankton production is not usually limited by nutrient availability while the lake is homothermous (i.e. when there is little variation in temperature with depth). However, surface concentrations of nitrogen and phosphorus are often low during stratification (Reynolds 1976). When lakes experience persistent stratification, the hypolimnion can become anoxic and nutrient rich (Bormans & Condie 1998). Temperature has also been considered an important factor in

influencing phytoplankton succession because of effects on phytoplankton growth rates and resource utilization (Tilman et al. 1982). Cyanobacteria can dominate phytoplankton communities at high water temperatures (Robarts & Zohary 1987), usually between 15-30°C (Haider et al. 2003). Since high temperatures often coincide with the onset of thermal stratification, the effects of temperature and stratification can become confounded (Reynolds & Walsby 1975). Because of these changes in chemical concentrations and distributions, discontinuities in phytoplankton populations would also be expected. In stratified systems, surface blooms often form as buoyant phytoplankton migrate diurnally to the epilimnion to receive more light for photosynthesis, while heavier species, such as diatoms, tend to sink out of the water column (Sherman et al. 1998).

2.3.2 Cyanobacteria dominance

The dominance of cyanobacteria has been linked to a number of factors including buoyancy regulated movement (Reynolds & Walsby 1975), optimal physiology and growth at high temperatures (Robarts & Zohary 1987), and the ability to fix nitrogen. They thus have an advantage under low nitrogen to phosphorus ratios (Smith 1983). In deep, monomictic, temperate lakes, thermal stratification signifies the succession of phytoplankton populations from diatoms to green algae and concludes with summer dominance of cyanobacteria or dinoflagellates (Oliver & Ganf 2000). The two environmental factors that are thought to promote this succession are thermal stratification and nutrient availability (Reynolds 1984). Grazing by zooplankton has also been shown to influence phytoplankton species succession towards dominance by cyanobacteria (Sterner 1989). Zooplankton can exert direct (grazing) effects on phytoplankton community structure as well as indirect effects through nutrient recycling (Bergquist & Carpenter 1986; Lehman & Sandgren 1985; Sterner 1986). However, studies investigating the ability of zooplankton to consume cyanobacteria have had inconclusive results (de Bernardi & Giussani 1990). Toxins from cyanobacteria have been shown to effect herbivores (Christoffersen & Burns 2000) and some cyanobacteria could be difficult to consume due to the shape and large size of colonies (Porter & McDonough 1984; Webster & Peters 1978). Cyanobacteria may then have an advantage over other phytoplankton by escaping from high grazing pressure and by gaining access to the nutrients released in the process of the digestion of their competitors (Sterner 1986).

2.3.3 The Lower Karori Reservoir

The Lower Karori Reservoir is a warm monomictic lake, as it has summer stratification and circulates fully in winter with temperatures above 4°C (Jolly & Irwin 1975). The Lower Karori Reservoir is within a 252 hectare 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 reservoir has an average depth of 8.2 m, a maximum depth of over 20 m and a total area of 2.5 ha. It is orientated NE/SW and has a geographic centre of 41° 17' S and 174° 45' E. The catchment has been closed off to the public since 1906, before which it was mostly used 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 (*Perca fluviatilis*). Perch were introduced into the dam in 1878 by the Wellington Acclimatization Society (Thomson 1922). Juvenile perch are known to be zooplanktivorous both in New Zealand (Duncan 1967) and in their native Europe (Smyly 1952). 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). Perch populations in New Zealand are generally characterized 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 predators (McDowall 1990), high intraspecific competition (Duncan 1967), and possibly a lack of food sources (Deelder 1951). Under such conditions perch are known to form stunted populations consisting primarily of small fish (Alm 1946).

Blooms of cyanobacteria have occurred in the Lower Karori Reservoir for about the last eight years. The dominant bloom-forming species in the reservoir are *Anabaena lemmermannii* and *A. circinalis* (Wood 2005). These blooms have many detrimental effects on the sanctuary including possible risks to human and wildlife health. In this study I aimed to determine the

effects of thermal stratification on the physical, chemical and biological characteristics of the Lower Karori Reservoir. The specific aims of this part of the study were:

1. To determine how stratification influences dissolved oxygen, temperature, pH and nutrient dynamics in the Lower Karori Reservoir.
2. To monitor the phytoplankton and zooplankton communities through a seasonal stratification period in the reservoir, examining changes in the plankton communities associated with cyanobacterial blooms.
3. To examine the diet of different size classes of perch and relate the diet to the perch size class distribution and their potential influence on zooplankton populations within the reservoir.

2.4 MATERIALS AND METHODS

2.4.1 Field 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. Samples were taken 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 between 9 and 11 am. Two litres of water were taken at each sampling point. Samples were taken back to the laboratory within 2 hours 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, USA) at 1 m intervals from the surface to 10 m and at 2 m intervals from 10 m to 24 m. From February 2004 to June 2004, dissolved oxygen was not able to be recorded due to equipment failure. Water transparency was measured in the field at the three sites with a black and white Secchi disc.

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 regular occasions the net was set overnight for approximately 15 hours. The net was always retrieved early the next morning and all fish caught were immediately removed. Any live fish had euthanasia performed on them by way of pithing.

Captured fish were measured (standard length) to the nearest 1 mm and weighed to the nearest 0.1 g. All fish were then deep-frozen for later analysis, when fish were left to thaw before their stomachs were removed. The stomach contents of every fish were examined under a dissecting microscope at 40x magnification. All food items were identified to the lowest taxonomic level possible and counted.

2.4.2 Laboratory methods

To estimate phytoplankton abundance, a 50 ml subsample was taken from each 2 litre water sample and within 2 hours of collection was preserved with Lugol's solution. Phytoplankton abundance was estimated by cell counts using an inverted microscope and a sedimentation chamber (Ultermöhl 1958). For filamentous species the average number of cells per filament was calculated by averaging the number of cells in the first 20 filaments encountered. The total counts were standardized to cells ml^{-1} . Cyanobacteria were identified to species level, other phytoplankton were identified to genus level. Texts used for the identification of phytoplankton taxa were Baker & Fabbro (2002), Biggs & Kilroy (2000), Entwistle et al. (1997) and Moore (2000). A 500 ml subsample was preserved with 4% buffered borax formalin and used to estimate zooplankton abundance. The total number of individuals in a 500 ml subsample was counted and standardized to 1 litre. Organisms were counted and identified to the lowest possible taxonomic group using a dissecting microscope. Texts used for the identification of zooplankton taxa were Chapman & Lewis (1976) and Shiel (1995).

Water for dissolved nutrient analyses was filtered through 47 mm 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, ammonia, and dissolved phosphorous levels were determined using an Aqua Analyzer (Orbeco-Hellige model 952, Farmingdale, New York, USA).

2.4.3 Statistical analyses

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, USA). All statistical analyses were performed on $\log(x + 1)$ transformed

data to homogenize the variances. 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 after a Bonferroni adjustment. To compare relative plankton species abundances during times of stratification and times of complete circulation, plankton species abundance values were averaged over time to produce a site value. The stratification period used was between 12 November 2003 and 28 January 2004 (Figs. 2.1 & 2.2). The homothermous 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 for Windows (PRIMER-E Ltd, Plymouth, UK) on $\log(x + 1)$ transformed data was used to compare relative plankton species abundances during the two periods (Clarke & Warwick 2001). How closely the high-dimensional relationships among the samples are represented by the 2-dimensional plot is shown by the 'stress' value. The lower the stress level the more closely the relationships between samples are shown by the 2-dimensional non-metric MDS plot. 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. O'Dowd et al. 2003).

2.5 RESULTS

2.5.1 Physical and chemical dynamics

The onset of thermal stratification began in October, and ended in March (Fig. 2.1). The most severe stratification was in January, when surface temperatures reached 20°C and temperatures in the hypolimnion were around 12°C . The thermocline usually occurred in the top half of the water column, between 5 and 10 m. Thermal stratification was associated with reduced levels of dissolved oxygen in the hypolimnion, which were as low as 3.80 mg L^{-1} in December (Fig. 2.2). During the winter months the lake was homothermous with temperatures below 10°C and dissolved oxygen levels were high (above 12 mg L^{-1}) throughout the water column.

Fig. 2.1 Temperature (°C) depth profiles for the Lower Karori Reservoir over the 9-month period showing the onset of stratification during the summer period. Values are from the first sampling day of each month taken from the deepest point of the Lower Karori Reservoir. Note the increase in the depth of the epilimnion as the lake cools in autumn. Temperature was measured at 1 m intervals from the surface to 10 m and at 2 m intervals from 10 m to 24 m.

Fig. 2.2 Dissolved oxygen (mg L⁻¹) depth profiles for the Lower Karori Reservoir over the 9-month period showing reduced oxygen levels at depth during the summer months. Dissolved oxygen was measured at 1 m intervals from the surface to 10 m and at 2 m intervals from 10 m to 24 m. Values are from the first sampling day of each month taken from the deepest point of the Lower Karori Reservoir. The dissolved oxygen meter was broken during February to June; therefore, readings were not taken during this time.

Fig. 2.3 Average (a) total nitrogen (mg L⁻¹), (b) dissolved phosphorus levels (mg L⁻¹), (c) pH, and (d) Secchi disc depth (m) (± 1 standard error) for a 9month sampling period in the Lower Karori Reservoir. For dissolved phosphorus levels, concentrations for each depth averaged over the 3 sites are shown as these differences were significant. Total nitrogen and pH levels are averaged across all depths and sites as there were no significant differences. Secchi depth was measured at 3 sites in the reservoir on each occasion with a black and white Secchi disc.

Table 2.1 Results of a repeated measures ANOVA on $\log(x + 1)$ transformed data to determine the effects of depth and time on plankton abundance, nutrient concentrations and pH levels. Values are F statistics. $df_{\text{depth}} = 2$; $df_{\text{time}} = 21$; $df_{\text{time} \times \text{depth}} = 42$. To avoid a type I error a Bonferroni adjustment was performed on all tests as they came from the same data set (i.e. $0.05 / 6 \sim P < 0.01$).

	Between Subjects Effects	Within Subjects Effects	
	Depth	Time	Time x Depth
Cyanobacteria	0.828	55.420***	0.855
Total phytoplankton	1.656	45.477***	0.353
Total zooplankton	0.477	40.487***	0.534
Total nitrogen	0.358	1.308	0.007
Dissolved phosphorus	546.849***	2.396**	2.456***
pH	2.188	45.634***	1.099

** $P = 0.01 - 0.001$; *** $P < 0.001$

Table 2.2 Plankton taxa recorded in the Lower Karori Reservoir during the 9-month sampling period. Taxa are listed in order of abundance over the entire monitoring period.

Phytoplankton	Zooplankton
<i>Anabaena lemmermannii</i>	<i>Keratella</i> spp.
<i>Volvox</i> sp.	cf. <i>Polyarthra</i> spp.
<i>Anabaena circinalis</i>	<i>Bosmina meridionalis</i>
<i>Anabaena</i> cf. <i>inaequalis</i>	cf. <i>Trichocerca</i> sp.
<i>Tribonema</i> sp.	Copepod nauplii
<i>Asterionella</i> sp.	cf. <i>Filinia</i> sp.
<i>Closterium</i> sp.	<i>Asplanchna</i> sp.
<i>Staurastrum</i> sp.	Calanoid copepods
<i>Dictyosphaerium</i> sp.	Cyclopoid copepods
<i>Trachelomonas</i> sp.	<i>Daphnia carinata</i>
Naviculoid spp.	Chydoridae sp.
<i>Anabaena planktonica</i>	<i>Acarina</i> spp.
<i>Cryptomonas</i> sp.	Ostracod spp.
<i>Oocystis</i> sp.	<i>Ceriodaphnia dubia</i>
<i>Peridinium</i> sp.	
<i>Scenedemus</i> sp.	
<i>Cosmarium</i> sp.	

Total nitrogen levels over the entire nine month sampling period had a mean of 0.25 mg L⁻¹ with a slight peak at the end of January (Fig. 2.3a). Total nitrogen concentrations did not differ significantly over time ($P = 0.203$) or with depth ($P = 0.713$) (Table 2.1). Dissolved phosphorus had a mean of 0.02 mg L⁻¹ and showed considerable temporal and spatial variation (Fig. 2.3b). Dissolved phosphorus concentrations did change over time ($P = 0.004$) and with depth ($P = 0.008$) (Table 2.1). A significant depth x time interaction ($P < 0.001$, Table 2.1) indicated that at certain times dissolved phosphorus did differ significantly with depth but at other times did not. Concentrations were generally highest in the samples taken at 10 m and lowest at 2 m. Dissolved phosphorus levels were lowest at all depths during the summer and the most variation between depths occurred during autumn. Both total nitrogen and dissolved phosphorus were at moderate concentrations and were characteristic of mesotrophic lakes. The pH had a mean of 7.04 and fluctuated greatly with a range between 6.10 and 8.25 (Fig. 2.3c). Water clarity was at its lowest on 30 December 2003, with a Secchi disc depth of 0.90 m (Fig. 2.3d), when cyanobacteria abundance was at its highest. Mean Secchi depth of the entire sampling period was 1.86 m, and the greatest water clarity was on 12 November with a Secchi depth of 3.40 m.

2.5.2 Phytoplankton and zooplankton communities

Phytoplankton abundance peaked at the end of December at approximately 170 000 cells ml⁻¹ (Fig. 2.4). Cyanobacteria did not differ between depth samples throughout the sampling period ($P = 0.481$, Table 2.1) and constituted all of the peak phytoplankton density of 170 000 cells ml⁻¹ on 30 December 2004 (Fig. 2.5). A list of all plankton taxa recorded throughout this study is shown in Table 2.2. Four species of *Anabaena* were present in the Lower Karori Reservoir during the sampling period. Throughout the summer months the dominant species was *A. lemmermannii*. *Anabaena circinalis* and *A. cf. inaequalis* were present, but at lower densities. *Anabaena planktonica* was recorded for the first time in the Lower Karori Reservoir during the sampling period. It first appeared in samples on 4 February 2004 and stayed at low densities throughout the rest of the sampling period. Cyanobacteria dominated the samples during early summer but populations declined rapidly at the beginning of January (Fig. 2.6a). Total phytoplankton counts did not differ between depth samples either ($P = 0.267$) (Table 2.1). Large phytoplankton species (i.e. species larger than 30 µm) made up the greatest proportion of phytoplankton in the samples, particularly during the spring. Common species 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., made up a higher proportion of the plankton during the winter, but never dominated samples.

Total zooplankton abundance peaked at the end of December at around 3 500 specimens litre⁻¹ (Fig. 2.4), with no significant difference between depths ($P = 0.642$, Table 2.1). Rotifers were the most common zooplankton taxa during this peak and made up 90% of the species in the samples during stratification. Rotifers were the most frequently recorded zooplankton taxa throughout most of the sampling period (Fig. 2.6b). Common taxa were *Asplanchna* sp. and *Keratella* spp. Crustaceans became more dominant through the winter; particularly small crustaceans such as *Bosmina meridionalis*. Three species of limnetic Cladocera were recorded in the reservoir, *Bosmina meridionalis*, *Daphnia carinata* and *Ceriodaphnia dubia*. *Bosmina meridionalis* was the most abundant crustacean during the entire period. Large crustaceans were always present at low levels. *Daphnia carinata* was recorded at very low abundances, usually only about 5 specimens litre⁻¹. The slightly smaller *Ceriodaphnia dubia* was even less abundant. Chydorid species occurred in samples regularly. These species are normally littoral and benthic, but have been found to be related to the presence of filamentous phytoplankton, in particular cyanobacteria, to which they can adhere. 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 (all with P values < 0.001 , Table 2.1). Obvious reasons for this were because all abundances peaked during early the summer (Figs. 4 and 5). These tests did not have a significant time $\times$ depth interaction (Table 2.1), indicating similar plankton abundances throughout all layers in the reservoir during the entire sampling period. However, samples from the hypolimnion may not have been taken since the maximum depth of samples taken was 10 m.

Fig. 2.4 Average total phytoplankton (cells ml⁻¹) and total zooplankton (litre⁻¹) counts (± 1 standard error) for a 9-month period in the Lower Karori Reservoir. Open circles, left axis = phytoplankton counts. Closed circles, right axis = zooplankton counts.

Fig. 2.5 Average cyanobacteria (cells ml⁻¹) counts (± 1 standard error) for the 9-month sampling period in the Lower Karori Reservoir averaged across all depths and sites. Scale before break is log 10 and scale after break is linear.

Fig. 2.6 Seasonal changes in abundance of (a) phytoplankton and (b) zooplankton groupings in the Lower Karori Reservoir, as represented as a proportion of total phytoplankton and zooplankton abundance respectively.

Fig. 2.7 Non-metric multidimensional scaling (MDS, using 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. Closed squares = 2 m, stratification; Open squares = 2 m, no stratification; Closed circles = 6 m, stratification; Open circles = 6 m, no stratification; Closed triangles = 10 m, stratification; Open triangles = 10 m, no stratification. Stress = 0.1. For stratification, analysis of similarities, $P = 0.001$. For depth, analysis for similarities, $P = 1.00$.

Despite no significant effect of depth found in the ANOVA analysis, ANOSIM analyses showed that thermal stratification was associated with changes in plankton species composition (Fig. 2.7, stress = 0.1). Relative species composition differed significantly between times of stratification and times of complete water column mixing ($P = 0.001$), whereas no relationship was found between the distribution and abundance of plankton species and depth during either periods ($P = 1.00$). Both phytoplankton and zooplankton peaked during stratification and were at low abundances at other times.

2.5.3 Perch size structure and diet

The perch (*Perca fluviatilis*) population in the Lower Karori Reservoir appeared to be characterized by a large abundance of small, juvenile perch. Ninety five of the one hundred perch caught were between the sizes of 60 and 110 mm (Fig. 2.8a). The five perch caught that were longer than this were sized between 140 and 190 mm. The consumption of zooplankton appeared to be strongly related to the size of the perch (Fig. 2.8b). Zooplankton was the main source of food for the small fish. The large sized perch showed no evidence of having consumed zooplankton, but the sample size was small. These large perch mostly had empty stomachs but some had been consuming terrestrial invertebrates (e.g. larvae of Geometrid spp.). The diet of the smaller perch consisted of both zooplankton and macroinvertebrates (Fig. 2.9). Four main taxa of zooplankton were consumed, *Daphnia carinata*, *Ceriodaphnia dubia*, Cyclopoid copepods and Calanoid copepods. *Daphnia carinata* was the most commonly consumed taxa particularly during the autumn. During the summer copepods were more frequently consumed. These four species were the largest zooplankton taxa sampled from the lake during the study. Macroinvertebrates were also an important food source especially during the summer months. Almost all of the macroinvertebrates consumed were chironomid midge larvae.

Fig. 2.8 Size and diet of perch (*Perca fluviatilis*) in the Lower Karori Reservoir. (a) Length distribution of all perch caught during a 5 month sampling period. Length of perch was measured as standard length to the nearest mm. (b) Proportion of stomach contents that were zooplankton in relation to size of the perch.

Fig. 2.9 Diet composition of juvenile perch (*Perca fluviatilis*) caught in the Lower Karori Reservoir during a 5 month sampling period. For each sampling date the diet composition was averaged over all the perch caught on that date that had items in their stomachs and were between 60 and 110 mm. Numbers above bars indicate the number of perch. The black section of the bar indicates the proportion, by number, of the diet made up of macroinvertebrates and the white section, zooplankton.

2.6 DISCUSSION

2.6.1 Effects of thermal stratification on the phytoplankton community and chemical dynamics

A common occurrence in deep, monomictic, 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 stratification in the Lower Karori Reservoir, during November/December coincided with changes in phytoplankton species composition. Green algae (e.g. *Volvox* sp., *Staurastrum* sp.), yellow green algae (e.g. *Tribonema* sp.) and diatoms (e.g. *Asterionella* sp.) were the dominant taxa during the isothermal period. Water clarity was highest in spring. This “clear-water” phase is generally a consequence of high zooplankton grazing on phytoplankton and usually persists until species of phytoplankton that are inedible to the zooplankton become abundant (Sommer 1989). A bloom of cyanobacteria (with the dominant species being *Anabaena lemmermannii*) formed once the water column stabilized in December, and at its peak phytoplankton samples were composed of over 99% cyanobacteria. *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 point.

Thermal stratification in freshwater lakes may be directly related to phytoplankton succession and thus changes in their vertical distributions are also expected (Harris & Smith 1977). During times of stratification dissolved oxygen levels in the hypolimnion are reduced and this layer often becomes anoxic. In the epilimnion, nitrogen and phosphorus can fall to very low levels (Reynolds 1976). Only dissolved phosphorus concentrations varied with depth and time during this study. During the winter dissolved phosphorus levels differed with depth but were similar at all depths during the stratification period. Typically, phosphorus levels become elevated in the hypolimnion when a lake becomes stratified (Reynolds 1976). Total nitrogen concentrations were always at relatively low levels but increased after the collapse of the cyanobacterial bloom. Surface concentrations of ammonium are often temporarily raised following the breakdown of blooms (McCarthy 1980). *Anabaena* species are able to fix atmospheric nitrogen so low levels of nitrogen in the reservoir would not limit their growth. The pH values were highly variable over

time but not depth. Levels were generally always greater than 6, a condition that is known to coincide with cyanobacterial blooms (Haider et al. 2003).

There were no observed changes in vertical distribution of plankton populations, though the reason for this may be due to the depths of samples taken. The deepest samples were taken from 10 m. The bottom of the thermocline in the Lower Karori Reservoir sat at 10 m for the majority of the stratification period. This depth would have meant that many samples from the hypolimnion would not have been taken. This may also account for the unexpected dissolved phosphorus results. However, thermal stratification was still shown to affect the chemical and biological interactions within the lake. The occurrence of stratification was associated with reduced levels of dissolved oxygen in the hypolimnion, high temperatures in the epilimnion ($> 20^{\circ}\text{C}$, about the optimal temperature for cyanobacteria [Robarts & Zohary 1987]), and the development of the cyanobacterial bloom.

2.6.2 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 have shown that fish predation on zooplankton is high during spring and this shifts the zooplankton community towards dominance by smaller species (Sommer 1989). Large filter-feeding zooplankton taxa often decline in summer and are replaced by smaller taxa because the population mortality of smaller species is lower and their fecundity higher than large species during this period. 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. The succession of zooplankton from small to large taxa during summer through to autumn is possibly due to changes in phytoplankton composition paired with a slight reduction in fish predation (Sommer 1989). Large species, such as *Daphnia*, never dominated the zooplankton and were at particularly low levels during the summer. *Daphnia* is especially vulnerable to fish

predation, which can be high throughout the summer period as this is when juvenile fish are most abundant (Gliwicz & Pijanowska 1989).

2.6.3 The role of perch predation in structuring the zooplankton community and possible top-down effects on the phytoplankton

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

European perch are known to potentially undergo two diet 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 the perch in this study did not show discreet dietary shifts. Both zooplankton and benthic invertebrates (chironomid larvae) were important diet components for small perch. Seasonal variation in diet followed the availability of different species to the perch rather than the dietary switches seen in the Northern Hemisphere. Zooplankton was a major component of the perch diet, however, during the summer large zooplankton taxa were at relatively low levels and this was when benthic macroinvertebrates become more common in the diet. There was no evidence of piscivory in the few large perch caught and most 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; Deelder 1951). In the Lower Karori Reservoir, the perch population was dominated by perch between 60 and 110 mm. Planktonic zooplankton was a large component of the diet of these small fish. These small, juvenile perch could be having a substantial effect on the zooplankton community despite not being obligate planktivores, the effects of which could cascade through to the phytoplankton community.

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 (Oliver & Ganf 2000; Sterner 1989). However, the few studies that have been carried out in New Zealand have rejected the hypothesis that predation affects the structure of plankton communities (e.g. Chapman et al. 1985). Reasons for this result are the lack of planktivorous predators in New Zealand and that crustacean zooplankton often appear food limited (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). The densities of perch in the reservoir were not known but the netting survey indicates that the population was dominated by small, juvenile fish. These fish were not exclusively zooplanktivorous and had an opportunistic diet which was dependent on the seasonal availability of prey. However, zooplankton were a major component of their diet and important larger, prey taxa (e.g. *Daphnia carinata* and *Ceriodaphnia dubia*) were always at low abundances in the lake, which may suggest strong effects of predation.

The cascading effects of fish on phytoplankton may be limited (Jeppesen et al. 2000). This is because New Zealand lakes tend to be dominated by phytoplankton taxa that are large celled and may be outside the feeding capacity of zooplankton (Burns 1998). In this study the phytoplankton community consisted mostly of taxa larger than 30 μm which are largely inedible to most zooplankton (Kerfoot et al. 1988). These large dominant phytoplankton taxa are often buoyant species that can control their position in the water column during thermal stratification (Malthus & Mitchell 1990). The fact that phytoplankton in New Zealand lakes may be poorly exploited by zooplankton may have flow-on effects. Malthus & Mitchell (1990) hypothesized that the unexploited phytoplankton could change the chemical composition and processes within the lake and shift the metabolism to the sediments. This nutrient shift would lead to high internal nutrient loading and increased sensitivity to external inputs.

2.7 CONCLUSIONS

The occurrence of cyanobacterial blooms in the Lower Karori Reservoir is probably the result of a number of factors. Nutrients within the lake are at relatively moderate levels, with low levels of nitrogen favouring nitrogen fixing cyanobacteria, such as the *Anabaena* species that dominate in the Lower Karori Reservoir. Predation pressure by perch (*Perca fluviatilis*) likely keeps large herbivorous zooplankton at low levels. The phytoplankton community is dominated by large phytoplankton (i.e. species larger than 30 µm) that are probably outside the grazing capacity of most zooplankton. The stability of the water column during the summer months favours buoyant cyanobacteria. 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. However, changes in cyanobacteria species composition may affect management strategies for the Lower Karori Reservoir. During the time period that this study was conducted the dominant bloom forming species was *Anabaena lemmermannii*. *Anabaena planktonica* was recorded for the first time in the reservoir in February 2004. By November 2004 *A. planktonica* had become the dominant bloom forming species (Wood 2005). Little is known about the ecology and physical requirements of this species but the occurrence of this species during the cooler months could indicate that bloom formation may arise earlier and for extended periods of time.

2.8 REFERENCES

- Allen, K. R. 1935: The food and migration of the perch (*Perca fluviatilis*) in Windermere. *Journal of Animal Ecology* 4: 264-273.
- Alm, G. 1946: Reasons for the occurrence of stunted fish populations with special regard to perch. *Report from the Swedish State Institute of Freshwater Research, Drottningholm* 25.
- Baker, P. D.; Fabbro, L. D. 2002: A guide to the identification of common blue-green algae (Cyanoprokaryotes) in Australian freshwaters. *Identification Guide No. 25. 2nd edition*. Canberra, Cooperative Research Centre for Freshwater Ecology. 43p.

- Bergquist, A. M.; Carpenter, S. R. 1986: Limnetic herbivory: effects on phytoplankton populations and primary production. *Ecology* 67: 1351-1360.
- Biggs, B. J. F.; Kilroy, C. 2000: Stream periphyton monitoring manual. Christchurch, New Zealand, NIWA. 227 p.
- Bormans, M.; Condie, S. A. 1998: Modelling the distribution of *Anabaena* and *Melosira* in a stratified river weir pool. *Hydrobiologia* 364: 3-13.
- Brooks, J. L.; Dodson, S. I. 1965: Predation, body size and composition of plankton. *Science* 150: 28-35.
- Burns, C. W. 1998: Planktonic interactions with an austral bias: implications for biomanipulation. *Lakes and Reservoirs: Research and Management* 3: 95-104.
- Chapman, M. A.; Green, J. D. 1987: Zooplankton ecology. In: Viner, A. B. ed. Inland waters of New Zealand. Wellington, New Zealand, DSIR Bulletin 241. Pp. 225-263.
- Chapman, M. A.; Green, J. D.; Jolly, V. H. 1975: Zooplankton. In: Jolly, V. H.; Brown, J. M. A. eds. New Zealand lakes. Auckland, Auckland University Press. Pp. 211-230.
- Chapman, M. A.; Green, J. D.; Jolly, V. H. 1985: Relationships between zooplankton abundance and trophic state in seven New Zealand lakes. *Hydrobiologia* 123: 119-136.
- Chapman, M. A.; Lewis, M. H. 1976: An introduction to the freshwater crustacea of New Zealand. Auckland, New Zealand, Collins. 261 p.
- Christoffersen, K.; Burns, C. W. 2000: Toxic cyanobacteria in New Zealand lakes and toxicity to indigenous zooplankton. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 27: 3222-3225.
- Clarke, K. R.; Warwick, R. M. 2001: Change in marine communities: an approach to statistical analysis and interpretation. Plymouth, UK, PRIMER-E.
- Craig, J. F. 1978: A study of the food and feeding of perch, *Perca fluviatilis* L., in Windermere. *Freshwater Biology* 8: 59-68.

- Cryer, M. 1988: Predatory impact of New Zealand smelt on natural populations of zooplankton. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 23: 1778-1783.
- de Bernardi, R.; Giussani, G. 1990: Are blue-green algae a suitable food for zooplankton? An overview. *Hydrobiologia* 200/201: 29-41.
- Deelder, C. L. 1951: A contribution to the knowledge of the stunted growth of perch (*Perca fluviatilis* L.) in Holland. *Hydrobiologia* 3: 357-378.
- Duncan, K. W. 1967: The food and population structure of perch (*Perca fluviatilis* L.) in Lake Mahinerangi. *Transactions of the Royal Society of New Zealand, Zoology* 9: 45-52.
- Entwistle, T. J.; Sonneman, J. A.; Lewis, S. H. 1997: Freshwater algae in Australia: guide to conspicuous genera. Sainty & Associates, Potts Point, Australia. 242 p.
- Gliwicz, Z. M. 1990: Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 83-97.
- Gliwicz, Z. M.; Pijanowska, J. 1989: The role of predation in zooplankton succession. In: Sommer, U. ed. *Plankton ecology: succession in plankton communities*. Berlin, Springer-Verlag. Pp. 253-296.
- Haider, S.; Naithani, V.; Viswanathan, P. N.; Kakkar, P. 2003: Cyanobacterial toxins: a growing environmental concern. *Chemosphere* 52: 1-21.
- Hall, D. J.; Threlkeld, S. T.; Burns, C. W.; Crowley, P. H. 1976: The size-efficiency hypothesis and the size structure of zooplankton communities. *Annual Review of Ecology and Systematics* 7: 177-208.
- Harris, G. P.; Smith, R. E. H. 1977: Observations of small-scale spatial patterns in phytoplankton populations. *Limnology and Oceanography* 22: 887-899.
- Jellyman, D. J. 1980: Age, growth, and reproduction of perch, *Perca fluviatilis* L., in Lake Pounui. *New Zealand Journal of Marine and Freshwater Research* 14: 391-400.
- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Burns, C. W. 1997: Do planktivorous fish structure the zooplankton communities in New Zealand lakes? *New Zealand Journal of Marine and Freshwater Research* 31: 163-173.

- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Christoffersen, K.; Burns, C. W. 2000: Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research* 22: 951-968.
- Jolly, V. H.; Irwin, J. 1975: Thermal conditions. In: Jolly, V. H.; Brown, J. M. A. eds. New Zealand lakes. Auckland, Auckland University Press. Pp. 90-105.
- Kerfoot, W. C.; Levitan, C.; DeMott, W. R. 1988: *Daphnia*-phytoplankton interactions: density-dependent shifts in resource quality. *Ecology* 69: 563-573.
- Lehman, J. T.; Sandgren, C. D. 1985: Species-specific rates of growth and grazing loss among freshwater algae. *Limnology and Oceanography* 30: 36-46.
- Lynch, J. 1995: Back to the future: Karori - from reservoir to wildlife sanctuary. *Forest and Bird* 12-19.
- Malthus, T.; Mitchell, S. F. 1990: On the occurrence, causes and potential consequences of low zooplankton to phytoplankton ratios in New Zealand lakes. *Freshwater Biology* 22: 383-394.
- Mazumder, A. 1994: Phosphorus-chlorophyll relationships under contrasting herbivory and thermal stratification: predictions and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 390-400.
- McCarthy, J. J. 1980: Nitrogen. In: Morris, I. ed. The physiological ecology of phytoplankton. Oxford, Blackwell. Pp. 191-233.
- McDowall, R. M. 1990: New Zealand freshwater fishes: a natural history and guide. Heinemann Reed. MAF Publication Group. 553 p.
- Moore, S. C. 2000: Photographic guide to the freshwater algae of New Zealand. Otago Regional Council, Dunedin, New Zealand. 77 p.
- O'Dowd, D. J.; Green, P. T.; Lake, P. S. 2003: Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6: 812-817.
- Oliver, R. L.; Ganf, G. G. 2000: Freshwater blooms. In: Whitton, B. A.; Potts, M. eds. The ecology of cyanobacteria. Kluwer Academic Publishers. Pp. 149-194.
- Porter, K. G.; McDonough, R. 1984: The energetic cost of response to blue-green algal filaments by cladocerans. *Limnology and Oceanography* 29: 365-369.

- Reynolds, C. S. 1976: Succession and vertical distribution of phytoplankton in response to thermal stratification in a lowland mere, with special reference to nutrient availability. *Journal of Ecology* 64: 529-551.
- Reynolds, C. S. 1984: The ecology of freshwater phytoplankton. Cambridge, Cambridge University Press. 384 p.
- Reynolds, C. S.; Walsby, A. E. 1975: Water-blooms. *Biological Review of the Cambridge Philosophical Society* 50: 437-481.
- Reynolds, C. S.; Oliver, R. L.; Walsby, A. E. 1987: Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *New Zealand Journal of Marine and Freshwater Research* 21: 379-390.
- Robarts, R. D.; Zohary, T. 1987: Temperature effects on photosynthetic capacity, respiration, and growth rates of bloom-forming cyanobacteria. *New Zealand Journal of Marine and Freshwater Research* 21: 391-399.
- Rowe, D. K.; Chisnall, B. L. 1996: Size-related differences in diel feeding activity, prey selection and nocturnal migration strategy for the planktonic larvae of *Gobiomorphus cotidianus* in Lake Rotoiti (NI), New Zealand. *Archiv für Hydrobiologie* 135: 485-497.
- Shapiro, J.; Lamarra, V.; Lynch, M. 1975: Biomanipulation: an ecosystem approach to lake restoration. In: Brezonik, P. L.; Fox, J. L. eds. Water quality management through biological control. Gainesville, University of Florida. Pp. 85-96.
- Sherman, B. S.; Webster, I. T.; Jones, G. J.; Oliver, R. L. 1998: Transitions between *Aulacoseira* and *Anabaena* dominance in a turbid river weir pool. *Limnology and Oceanography* 43: 1902-1915.
- Shiel, R. J. 1995: A guide to the identification of rotifers, cladocerans and copepods from Australian inland waters. Albury, NSW, Co-operative research centre for freshwater ecology. 144 p.
- Smith, V. H. 1983: Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671.
- Smyly, W. J. P. 1952: Observations on the food of the fry of perch (*Perca fluviatilis* Linn.) in Windermere. *Proceedings of the Zoological Society of London* 122: 407-416.

- Sommer, U. 1989: Toward a Darwinian ecology of plankton. *In: Sommer, U. ed. Plankton ecology: succession in plankton communities.* Berlin, Springer-Verlag. Pp. 1-8.
- Steffensen, D.; Burch, M.; Nicholson, B.; Drikas, M.; Baker, P. 1999: Management of toxic blue-green algae (cyanobacteria) in Australia. *Environmental Toxicology 14*: 183-195.
- Sterner, R. W. 1986: Herbivores direct and indirect effects on algal populations. *Science 231*: 605-607.
- Sterner, R. W. 1989: The role of grazers in phytoplankton succession. *In: Sommer, U. ed. Plankton ecology: succession in plankton communities.* Berlin, Springer Verlag. Pp. 107-170.
- Thomson, G. M. 1922: The naturalisation of animals and plants in New Zealand. London, Cambridge University Press. 607 p.
- Tilman, D.; Kilham, S. S.; Kilham, P. 1982: Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics 13*: 49-72.
- Webster, K.; Peters, R. H. 1978: Some size-dependent inhibitions of larger cladoceran filterers in filamentous suspensions. *Limnology and Oceanography 23*: 1238-1245.
- White, E. 1983: Lake eutrophication in New Zealand - a comparison with other countries of the Organisation for Economic Co-operation and Development. *New Zealand Journal of Marine and Freshwater Research 17*: 437-444.
- Wood, S. A. 2005: Bloom forming and toxic cyanobacteria in New Zealand: species diversity, distribution, cyanotoxin production and accumulation of microcystins in selected freshwater organisms. Unpublished PhD thesis, Victoria University and Massey University, Wellington, New Zealand. 306 p.

3. Cyanobacterial blooms appear to be driven by top-down rather than bottom-up effects in the Lower Karori Reservoir (Wellington)

3.1 Abstract The lower reservoir of the Karori Wildlife Sanctuary (Wellington) has experienced cyanobacterial blooms for the last eight years. In this study, I sought to test the role of nutrient resources (bottom-up) versus cascading effects of zooplanktivorous perch (*Perca fluviatilis*) (top-down) in controlling cyanobacteria in this lake. A 2 x 2 factorial field experiment was performed within plastic enclosures positioned in the lake, using two treatments: addition of juvenile perch and of nitrogen plus phosphorus. Four species of *Anabaena* were found with the dominant species being *A. lemmermannii*. Trichomes of *A. lemmermannii* were highly coiled and 3-4 µm broad. Cyanobacterial abundance was significantly higher in treatments with perch. The addition of nutrients had no significant effect on cyanobacterial densities, but there was a weak fish ? nutrient interaction on cyanobacteria abundance. There was no overall difference in zooplankton abundance under any of the treatments but zooplankton species diversity was higher in treatments without perch. Community composition of both phytoplankton and zooplankton species was altered by all treatments. My results suggest that an eradication of perch may cause a reduction in cyanobacteria abundance with the plankton being dominated by both larger phytoplankton and zooplankton species.

3.2 Keywords Cyanobacteria; *Anabaena*; top-down; bottom-up; *Perca fluviatilis*; nitrogen; phosphorus; Karori Wildlife Sanctuary

3.3 INTRODUCTION

Freshwater blooms of cyanobacteria have become a significant problem in New Zealand (Wood 2005) and around the world (e.g. Steffensen et al. 1999). They are commonly associated with increased nutrient enrichment of inland waters as a result of more intensive industrial and agricultural practices (Carpenter et al. 1998). Blooms are associated with strong odours, water discolouration and surface scums. More importantly, they pose a possible risk to wildlife and human health if toxins are produced (Flint 1966). More than 40 species of cyanobacteria produce toxins worldwide, although the conditions under which cyanobacteria produce toxins still remain unclear (Haider et al. 2003).

The adverse effects associated with cyanobacterial blooms and lake degradation has resulted in a rising interest in lake restoration research. Traditionally, efforts have been aimed towards reducing nutrient inputs (Schindler 1974), as popular models assumed that ecosystems were principally regulated from the “bottom-up” (White 1978). However, reversing the effects of eutrophication can be expensive and not always successful. For many lakes, nutrient inputs cannot be easily controlled (Carpenter et al. 1998) or they have been eutrophic for so long that their sediments begin to act as a source of nutrients rather than a sink (Shapiro et al. 1975).

Nutrient supply alone cannot explain all the variation in primary production of the world’s lakes (Schindler 1978). The trophic cascade concept was proposed to explain differences in productivity of lakes with similar nutrient levels, but with differing food webs (Carpenter et al. 1985). This “top-down” concept has been extensively studied in freshwater ecosystems, leading to the proposal that by manipulating the food web, primary production could be controlled (cf. pioneer works of Zaret & Paine 1973, Shapiro et al. 1975). Manipulating food webs could thus be a useful lake restoration tool. By decreasing the abundance of zooplanktivorous fish, the abundance of large herbivorous zooplankton should increase, and phytoplankton biomass should decrease, due to more intensive grazing by these herbivores (Carpenter & Kitchell 1993). This food web manipulation was proposed as a solution for lakes where nutrient input is fixed or cannot be significantly reduced (Shapiro et al. 1975).

It was originally considered that these two models (bottom-up versus top-down) were mutually exclusive; however, they can actually be complementary. More recent research has tried to fuse these two models as it became obvious that one-dimensional models were insufficient in explaining food chain dynamics (Persson et al. 1992). Instead, research has looked to examine the relative strengths of top-down and bottom-up forces in food webs (Leibold et al. 1997; McQueen et al. 1986; Oksanen et al. 1981; Jeppesen et al. 2000). Researchers have theorized that potential productivity at all levels of a food web is set by resources and the actual productivity depends on trophic interactions (Carpenter et al. 1985).

The Lower Karori Reservoir, situated within the Karori Wildlife Sanctuary in Wellington, has experienced cyanobacterial blooms for approximately the last eight years. The first severe bloom occurred during the summer of 2000/01. The aim of this present study was to experimentally manipulate and elucidate the role of nutrients (bottom-up) and the effects of fish as zooplankton consumers (top-down) in controlling cyanobacterial blooms in the Lower Karori Reservoir. The following hypotheses were tested:

1. High levels of nutrients promote cyanobacterial blooms.
2. The cascading effects of zooplanktivorous fish promote cyanobacterial blooms.
3. Cyanobacterial blooms are caused by a combination of both bottom-up and top-down factors.

3.4 MATERIALS AND METHODS

3.4.1 Study site

The Lower Karori Reservoir was completed in 1874 as part of the first water supply scheme for Wellington City. The reservoir has an average depth of 8.2 m, a maximum depth of over 20 m and a total area of 0.025 km². There are two exotic species of fish in the Lower Karori Reservoir, brown trout (*Salmo trutta*) and European perch (*Perca fluviatilis*). Perch were introduced into the reservoir in 1878 by the Wellington Acclimatization Society (Thomson 1922). Juvenile perch are known to consume zooplankton both in New Zealand (Duncan 1967) and their native Europe (Smyly 1952). Perch are well known to form stunted populations of small fish (Alm 1946) and populations in New Zealand are generally characterized by large populations of small fish despite

their potential to reach large size (Duncan 1967). The perch population in the Lower Karori Reservoir is dominated by small, juvenile perch that could be having a strong effect on the plankton community (see Chapter Two).

3.4.2 Experimental design and field methods

Eight 1 m x 1 m x 2 m enclosures were built out of wooden frames, covered in polyethylene plastic sheets and buoyed with floats (Fig. 3.1). The enclosures were placed haphazardly in a sheltered area of the lake and anchored to the lake bottom. They were open to the surface and closed off at the base to mimic the pelagic zone of the lake. The tops were covered in 13 mm wire mesh in order to stop fish from escaping or predation by birds. Enclosures were filled on 11 February 2004 by lowering the enclosures from about 2 m depth to the surface. Experiments were initiated on 2 March 2004 according to a 2 x 2 factorial design using two treatments: addition of 3 juvenile perch (1.5 fish m^{-3} , sized between 60 and 110 mm), and addition of nitrogen (60 g of N as NH_4NO_3) plus phosphorus (6 g of P as KH_4PO_4). The four treatment combinations were absence of perch and nutrient additions (control), absence of perch and the addition of nutrients, presence of perch with nutrients, and presence of perch with no nutrients. The nutrients were added at a 10:1 N:P mass ratio as this was the ambient ratio mass ratio of nitrogen : phosphorus in the lake. The exact density of juvenile perch in the lake was unknown; however, 1.5 fish m^{-3} is similar to densities of perch of the same size used in other enclosure studies (e.g. Mazumder et al. 1988; Romare et al. 1999). Two replicates of each treatment combination were randomly assigned to the enclosures. More replicates were not possible due to the costs of constructing further enclosures and time restrictions.

Fig. 3.1 Plastic enclosures used in the food web field manipulation experiment.

Perch for the experimental enclosures were caught with 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. Perch were netted within the lake over a period of two weeks, until 12 perch were caught that were between 60 and 100 mm of length. Perch were kept alive in lake water at ambient lake temperature in glass tanks in a laboratory at Victoria University (Wellington). Additionally, perch were suspended in the lake within buckets to acclimatize to lake conditions before being released into the enclosures. Nutrients were first dissolved in water from the enclosure to which they were being added. The enclosures were mixed briefly with an oar following the addition of nutrients to ensure even distribution. All fish and one dose of nutrients were added at the beginning of the experiment (2 March 2004, Day 0). Another dose of nutrients was added part way through (16 March 2004, Day 14). Water samples were taken immediately before the addition of nutrients. This dosage of nutrients meant that nutrient levels increased from mesotrophic levels (i.e. ambient lake levels, see Chapter Two) to levels seen in eutrophic lakes (see Figs. 3.2a and b). The experiment was terminated on 26 March 2004, Day 24.

Fig. 3.2 Mean (a) total nitrogen and (b) dissolved phosphorus (mg L^{-1}) (± 1 standard error) under each treatment. Dates where treatments were added are marked with an asterisk. On 2 March 2004 all fish and 1 dose of nutrients was added. On 16 March 2004 another dose of nutrients was added. Nutrient levels increased from mesotrophic (ambient) levels to eutrophic levels.

Water samples were always taken between 0900 and 1100 from the centre of the enclosures at approximately 1 m depth with a transparent 2-litre self-activating plankton trap. One set of samples was taken immediately prior to the beginning of the experiment (2 March 2004, Day 0). Samples were taken every 3-4 days for 24 days after the addition of the treatments. Two replicate samples of 2-litres were taken from every enclosure each trip. Samples were taken back to the laboratory within 2 hours 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, USA). Dissolved oxygen was not able to be recorded throughout the entire experiment because of equipment breakdown. Water clarity was measured with a black and white Secchi disc. If the bottom of the enclosure was visible, Secchi depth was recorded as 2 m. On each sampling trip the enclosures were carefully checked for dead fish. Two fish died during the duration of the experiment, one from the treatment of perch plus nutrients (9 March 2004, Day 7) and another from the treatment of perch without nutrients (12 March 2004, Day 10). The dead fish were not replaced.

3.4.3 Laboratory methods

From each 2-litre water sample a 50 ml subsample was taken for phytoplankton abundance analysis and preserved within 2 hours of collection with Lugol's solution. Cell counts were estimated using an inverted microscope and a settling chamber (Utermöhl 1958). The whole chamber was scanned at 200x magnification. For filamentous species the average number of cells per filament was calculated by averaging the number of cells in the first 20 filaments encountered. The total counts were then standardized to cells ml⁻¹. Cyanobacteria were identified to species, other phytoplankton were identified to genus level. Texts used for the identification of phytoplankton taxa were Baker & Fabbro (2002), Biggs & Kilroy (2000), Entwistle et al. (1997), and Moore (2000). Very large species of phytoplankton are poorly incorporated into planktonic food webs (Porter 1973). Phytoplankton may be resistant to grazing by zooplankton for many reasons, including size, shape, or taxonomic group (Bell 2002; Gliwicz 1990; Porter 1977). Phytoplankton taxa larger than 30 µm are mostly inedible to common zooplankton species (Burns 1968). Size can thus give an approximate indication of phytoplankton edibility. The size structure of the phytoplankton communities was examined by combining phytoplankton species smaller than 30 µm (edible forms) from some analyses to determine the effects of zooplankton

grazing on phytoplankton community structure. For chlorophyll *a* determination, 1-litre subsamples were filtered through 47 mm Whatman GF/C glass microfibre filters and the filters frozen. Samples were analysed fluorometrically (Turner Designs 10-AU Fluorometer, Sunnyvale, California, USA) after soaking in methanol for 24 hours and corrected for pheopigments.

From each 2-litre sample a 500 ml subsample was preserved with 4% buffered borax formalin and used to estimate zooplankton abundance. The total number of individuals in a 500 ml subsample was counted and standardized to 1-litre. Organisms were counted and identified to the lowest possible taxonomic group using a dissecting microscope at 40x magnification. Texts used for the identification of zooplankton taxa were Chapman & Lewis (1976) and Shiel (1995). Large zooplankton taxa are more vulnerable to predation by visually feeding planktivorous fish (Brooks & Dodson 1965). By combining large species of zooplankton (i.e. *Daphnia carinata*, *Ceriodaphnia dubia*, cyclopoid copepods and calanoid copepods) that are preyed upon by perch for some analyses the effects of perch predation on zooplankton community structure was examined.

Water for dissolved nutrient analyses was filtered through pre-washed 47 mm Whatman GF/C glass microfibre filters. Filtered water was stored frozen in clean polyethylene bottles. Nitrate, nitrite, ammonia, and dissolved phosphorous levels were determined using an Aqua Analyzer (Orbeco-Hellige model 952, Farmingdale, New York, USA).

3.4.4 Statistical analysis

Phytoplankton and zooplankton species diversity was calculated using the Shannon-Weiner diversity index (H'), which has the following formula:

$$H' = - \sum_{i=1}^S (P_i \ln[P_i])$$

where P_i is the proportion of individuals found in the i_{th} species and $\ln$ is the natural logarithm.

Repeated measures analysis of variance was used to compare the effects of treatments on plankton populations over time using SPSS 11.15 for Windows (SPSS Inc., Chicago, USA).

Day 0 was excluded from the analysis as this date was part of the pre-treatment period. The two replicate samples from within each enclosure taken on each sampling occasion were averaged to avoid pseudoreplication. The time trial factor (number of sampling dates) was the dependent variable. All statistical analyses were performed on $\log(x + 1)$ transformed data to homogenize the variances. The possibility of a Type I error occurring when a number of tests is performed on the same data set is high. So for tests that used phytoplankton and zooplankton counts, P values < 0.01 were considered to be statistically significant after a Bonferroni adjustment because these tests came from the same sample. Of the 9 tests in Table 3.1, 5 had a Bonferroni adjustment as they tested different aspects of the same sample. For all other tests, P values < 0.05 were considered statistically significant. A one-way ANOVA was performed on Day 0 cyanobacterial densities to ensure initial cyanobacteria densities were similar within all enclosures.

In addition, for each enclosure, species abundance values were averaged over time after the initiation of the experiment (i.e. Days 3-24) to produce a site value. I used non-metric multidimensional scaling (using a Bray-Curtis dissimilarity coefficient) followed by analysis of similarities (ANOSIM) on $\log(x + 1)$ transformed data to compare relative plankton species abundances in the eight enclosures (Clarke & Warwick 2001). Primer 5 for Windows (PRIMER-E Ltd, Plymouth, UK) was used for these analyses. How closely the high-dimensional relationships among the samples are represented by the 2-dimensional plot is shown by the 'stress' value. The lower the stress level the better the relationships between samples are shown by the 2-dimensional non-metric MDS plot. ANOSIM was used to test for similarity of species composition under each of the treatments. These analyses are commonly used to examine similarities between species assemblages (e.g. O'Dowd et al. 2003).

3.5 RESULTS

Initial cyanobacterial densities in the enclosures were shown to be significantly different (one-way ANOVA, $df = 7$, $P = 0.023$). However, post-hoc tests (Tukey test) showed no significant differences between any of the enclosures. These discrepancies were probably due to the lower densities of cyanobacteria in the control treatment. Cyanobacterial densities were highest in enclosures with perch (*Perca fluviatilis*) (Fig. 3.3). Four species of cyanobacteria were

recorded, *Anabaena lemmermannii*, *A. circinalis*, *A. cf. inaequalis*, and *A. planktonica*. The dominant species was initially *A. lemmermannii*, with a switch to *A. planktonica* towards the conclusion of the experiment. Other cyanobacteria species were mostly rare. *Anabaena planktonica* was recorded in the Lower Karori Reservoir for the first time this season. Trichomes of *A. lemmermannii* were high coiled and approximately 3-4 μm broad. Trichomes of *A. planktonica* were straight and approximately 8.5-12 μm broad. Cyanobacteria in all treatments declined over time (Table 3.1, Fig. 3.3), but this is thought to be a seasonal effect as it was nearing the end of summer. For simplicity, other results have been summarized to grand means for the duration of the experiment after the addition of treatments (Fig. 3.4). Significantly higher densities of cyanobacteria were observed in the presence of perch ($P = 0.003$) (Fig. 3.4a, Table 3.1). Despite there being no directly significant effect of nutrients, a marginally significant perch x nutrient interaction occurred ($P = 0.032$, this was not significant after a Bonferroni adjustment), indicating that when perch were added higher levels of cyanobacteria occurred in the treatment without added nutrients.

Though there was no statistically significant effect of any of the treatments on total phytoplankton cells ml^{-1} (Fig. 3.4b, Table 3.1), chlorophyll *a* levels were marginally significantly higher in nutrient treatments at the $P = 0.010$ level (Fig. 3.4c, Table 3.1). Perch addition did not have a statistically significant effect on chlorophyll *a* ($P = 0.333$). Species composition differed under each of the treatments. The control treatment was dominated by large species (i.e. species larger than 30 μm) in particular *Volvox* sp. The nutrient regime in the experiment did not favour *Anabaena* spp. and treatments with nutrient additions were dominated by smaller species (e.g. *Cryptomonas* sp. and *Scenedemus* sp.). After the second addition of nutrients, *Kirchneriella* sp. appeared in samples from several of the nutrient treatment enclosures. The phytoplankton community in the treatment with only perch consisted of these small species and also large species (e.g. *Closterium* sp.). There was a significant effect of both perch ($P < 0.001$) and nutrient addition ($P = 0.001$) on edible algae (i.e. cells $< 30 \mu\text{m}$). The experimental treatments did not statistically affect phytoplankton species diversity (Fig. 3.4e). Water clarity (as Secchi depth) was significantly reduced with the addition of perch ($P = 0.019$) (Fig. 3.4f) and at a = 0.10 level with the addition of nutrients ($P = 0.078$).

Total zooplankton abundance was not statistically different under any of the treatments (Fig. 3.5a), although abundance decreased significantly over time (Table 3.1), possibly due to seasonal effects. From analyses of perch diet in the Lower Karori Reservoir (see Chapter Two) it was shown that perch were consuming four main zooplankton taxa, *Daphnia carinata*, *Ceriodaphnia dubia*, Cyclopoid copepods and Calanoid copepods. These taxa are the largest zooplankton present in the reservoir and are more vulnerable to predation by visually feeding planktivorous fish. When all other smaller species of zooplankton (such as rotifers and small crustaceans) were removed from the analysis (Fig. 3.5b) large zooplankton densities were marginally significant in the absence of perch at $\alpha = 0.05$ ($P = 0.058$), although not after a Bonferroni adjustment. The reduction of large crustaceans was compensated by an increase in rotifers such that there was no overall difference in total zooplankton abundance. Zooplankton species diversity was much lower in treatments with perch ($P = 0.049$) (Fig. 3.5c). Nutrients did not have a significant effect on diversity ($P = 0.347$).

The relative species composition of plankton under each of the treatments differed significantly at the $P < 0.10$ level and almost so at the $P < 0.05$ level (Fig. 3.6, stress = 0.06, ANOSIM $P = 0.067$). Pairwise comparisons (Table 3.2) show that none of the groups were significantly different. However, the pairwise R statistic can be much more important, particularly when there are a low number of replicates as with this study (Clarke & Warwick 2001). Most of the treatments are well separated from each other ($R > 0.75$). Species composition in the treatment, nutrients and fish, is indistinguishable from the treatments of either nutrients, or fish ($R < 0.25$). All of the treatments caused a shift in plankton community composition, with the treatment of nutrients and fish being similar to other treatments that had the addition of fish or nutrients.

Fig. 3.3 Mean cyanobacteria (cells ml⁻¹) levels ($\pm$ 1 standard error) under each treatment. Dates where treatments were added are marked with an asterisk. On 2 March 2004 all fish and 1 dose of nutrients was added. On 16 March 2004 another dose of nutrients was added.

Table 3.1 Results of repeated measures ANOVA on log(x + 1) transformed data to determine the effects of nutrient and fish additions on phytoplankton and zooplankton populations. Values are F statistics and df = 7. To avoid a type I error a Bonferroni adjustment was performed on tests that used phytoplankton or zooplankton counts from the same data set. *Italic values indicate values for these tests that are still statistically significant after a Bonferroni adjustment (i.e. 0.05 / 5 = P < 0.01).*

	Between Subjects Effects				Within Subjects Effects		
	Fish	Nutrients	Fish x Nutrients	Time	Time x Fish	Time x Nutrients	Time x Fish x Nutrients
Total phytoplankton†	1.057	0.965	0.392	2.349	0.634	<i>4.605**</i>	1.424
Cyanobacteria†	<i>38.857**</i>	1.779	10.500*	<i>25.602***</i>	<i>4.140**</i>	1.573	2.249
Chlorophyll a	1.211	21.305*	0.106	9.185***	5.210**	<i>24.555***</i>	1.069
Edible phytoplankton (<30 µm)†	<i>219.650***</i>	<i>85.999**</i>	<i>54.167**</i>	<i>5.343**</i>	<i>3.894**</i>	<i>9.568***</i>	<i>10.674***</i>
Phytoplankton species diversity	0.597	3.204	4.968	4.431**	2.191	5.678**	3.518*
Secchi disc depth	14.451*	5.561	7.891*	<i>7.516***</i>	2.206	0.110	2.317
Total zooplankton†	4.433	0.043	1.859	<i>9.956***</i>	0.307	1.191	<i>4.396**</i>
Large zooplankton†	6.924	4.898	2.562	2.424	2.131	0.623	<i>5.803**</i>
Zooplankton species diversity	7.802*	1.136	0.024	0.799	3.003*	1.512	1.310

P* = 0.05 – 0.01; *P* = 0.01 – 0.001; ****P* < 0.001

† Tests which have had a Bonferroni adjustment

Fig. 3.4 Grand mean values over experiment duration (± 1 standard error). (a) Cyanobacteria (cells ml^{-1}), (b) Total phytoplankton (cells ml^{-1}), (c) Chlorophyll a ($\mu\text{g litre}^{-1}$), (d) Edible phytoplankton (cells ml^{-1}), (e) Phytoplankton species diversity (H' , Shannon-Weiner diversity index), and (f) Secchi disc depth (m). P values are between subjects effects and are derived from repeated measures ANOVA on $\log(x + 1)$ transformed data.

Fig. 3.5 Grand mean values over experiment duration (± 1 standard error). (a) Total zooplankton (litre⁻¹), (b) Large zooplankton (litre⁻¹), and (c) Zooplankton species diversity (H' , Shannon-Weiner diversity index). P values are between subjects effects and are derived from repeated measures ANOVA on $\log(x + 1)$ transformed data.

Fig. 3.6 Non-metric multidimensional scaling (MDS, Bray-Curtis dissimilarity) on $\log(x + 1)$ transformed data of relative species composition of the eight experimental enclosures. Closed squares = Control; Open squares = Nutrients; Open circles = Nutrients and fish; Closed circles = Fish. Overlapping points are offset with a vertical line separating. Stress = 0.06.

Table 3.2 Pairwise Test comparisons for analysis of similarities (ANOSIM) on $\log(x + 1)$ transformed data. Global $R = 0.479$, $P = 0.067$. $R > 0.75$ well separated, $R > 0.5$ overlapping but different, $R < 0.25$ no difference between treatments.

Groups	R Statistic	Significance Level
Control, Nutrients	0.75	0.33
Control, Nutrients + fish	0.50	0.33
Control, Fish	1.00	0.33
Nutrients, Nutrients + fish	-0.25	0.67
Nutrients, Fish	1.00	0.33
Nutrients + fish, Fish	0.00	1.00

3.6 DISCUSSION

Perch had a significant effect on cyanobacteria levels in the Lower Karori Reservoir. Cyanobacteria levels were highest in the treatment with only the presence of perch (*Perca fluviatilis*). Cyanobacteria levels may not have been as high in the treatment with the addition of perch and nutrients because of the addition of high levels of nitrogen. *Anabaena* spp. have the ability to fix atmospheric nitrogen and may have lost some competitive advantage over other phytoplankton when nitrogen levels within the enclosures were elevated (Smith 1983).

Planktivorous fish are known to selectively consume large zooplankton and shift zooplankton communities towards dominance by smaller species, such as rotifers (Gliwicz & Pijanowska 1989). This change in zooplankton composition is often followed by a shift in phytoplankton community structure toward dominance by cyanobacteria (Vanni & Findlay 1990). The positive effect on cyanobacteria by planktivorous fish can not always be explained by changes in grazing pressure by zooplankton (Vanni & Layne 1997) since there are doubts over the edibility of filamentous cyanobacteria (Gliwicz 1990). Enhanced phytoplankton production in the presence of planktivorous fish may instead be due to changes in nutrient cycling. Fish also excrete and egest nutrients directly to phytoplankton (Brabrand et al. 1990). In this study, nutrient recycling and grazing pressure were not measured so it is not known by which mechanism perch affected *Anabaena* growth. Nutrient recycling by fish may be especially important in lakes that have low external phosphorus inputs yet have a high abundance of small planktivorous fish (Vanni & Layne 1997) as in this case. The release of nutrients by fish could have a large effect on phytoplankton species that need high supply rates of phosphorus, such as cyanobacteria (Attayde & Hansson 2001).

In this experiment, the exclusion of perch caused a marginally significant increase in abundance of large crustaceans that are the main prey for perch in this lake (see Chapter Two), in particular the cladoceran *Daphnia carinata*. Large *Daphnia* have the highest rates of phytoplankton removal from the water column of all zooplankton species (Peters & Downing 1984). In the control treatment the increase in abundance of large crustaceans was correlated with an increase in large phytoplankton species. A lot of the phytoplankton taxa that cause water quality problems

in New Zealand are large celled or colonial species that may be difficult for zooplankton to consume (Burns 1998). The large phytoplankton species that dominated the control treatment are presumably outside the grazing capacity of even the largest species of zooplankton, such as *Daphnia carinata*. Despite the inability of zooplankton to reduce the abundance of these large phytoplankton species, these large phytoplankton may still be more desirable than cyanobacteria. Phytoplankton counts for the control treatment were not statistically different to the other treatments but the control had the lowest levels of cyanobacteria and the highest water clarity.

Changes in phytoplankton species compositions under each of the treatments can also be revealed by differences in chlorophyll *a* levels. While phytoplankton cell counts were not statistically different in any of the treatments, chlorophyll *a* levels were much higher in treatments with nutrient additions, indicating higher phytoplankton biomass in the nutrient treatments. Chlorophyll *a* content in phytoplankton varies between species (Viner & White 1987). Treatments with nutrient additions had higher abundance of phytoplankton species that have high chlorophyll *a* content (e.g. *Cryptomonas*) (Reynolds 1984). The control and perch treatments had many species with low chlorophyll *a* content per cell (e.g. *Staurastrum* and *Anabaena* respectively) (Reynolds 1984). The treatments promoted the growth of different types of phytoplankton and caused species composition changes that differed in chlorophyll *a* content. The control treatment was dominated by large forms that are not readily consumed by zooplankton but still had high water clarity. Treatments with nutrient additions were characterized by small species with high chlorophyll *a* content and reduced water clarity, while the perch treatment was dominated by cyanobacteria. Nutrient additions favoured small phytoplankton taxa suggesting that the ratio or amount of nutrients added were not favourable to cyanobacteria. *Anabaena* species can fix atmospheric nitrogen and so are less limited by lake nitrogen levels than other phytoplankton. When nitrogen was added to the enclosures *Anabaena* species may have lost a competitive advantage over other phytoplankton taxa.

The size distribution of the filter-feeding herbivores also determines the vulnerability of the phytoplankton community to grazing. Large species of zooplankton, such as *D. carinata* can graze a broader range of phytoplankton size classes and morphologies (Sterner 1986) and are the most effective in controlling phytoplankton blooms (Leibold 1989). These large species are more

vulnerable to predation by planktivorous fish, often increasing in abundance with the removal of these fish (Brooks & Dodson 1965). Total zooplankton abundance in this experiment did not differ between treatments but there was a shift in the relative abundance of different species. In treatments with perch, a decrease in large zooplankton meant that rotifers and small crustaceans increased in abundance so that no overall differences in total zooplankton abundance occurred during the duration of the experiment. The changes in zooplankton abundances possibly meant that the zooplankton communities were exerting differing levels of grazing pressures on the relative phytoplankton communities. Zooplankton communities dominated by small-sized zooplankton would consume a smaller range of phytoplankton sizes and morphologies, and would be less effective in controlling phytoplankton blooms.

Within-lake enclosures, as employed in this study, have been widely used in aquatic ecology. Yet there is still doubt over whether they adequately simulate lake trophic interactions (Carpenter 1996, Benndorf et al. 2002, but see Drenner & Mazumder 1999). Results from enclosure studies can be misleading if not backed up by larger field studies and the major criticism of enclosure studies is spatial and temporal scale. The enclosures must be large enough to reflect the physical characteristics of the lake, hold realistic densities of fish (Vanni et al. 1997) and experiments should be able to observe long term trends (Carpenter 1996). For this experiment natural perch densities within the lake were not known, so the effects of perch may have been exaggerated. However, the density was typical of similar studies using juvenile perch, as was the enclosure size (e.g. Mazumder et al. 1988; Romare et al. 1999). Thermal and nutrient dynamics of the enclosures were similar to ambient lake conditions for the same depth. The duration of this experiment may have been too short to observe long-term trends, but still may be a useful indicator of the effects of the treatments on community dynamics (Carpenter 1996). Enclosure studies are regarded as a “black box” without the investigation of particular processes. However, this study was more concerned with the effects of treatments rather than the processes involved.

Despite these constraints, the results from this experiment suggest that an eradication of perch from within the Lower Karori Reservoir will likely cause a decrease in cyanobacterial blooms and an increase in water clarity, with the phytoplankton and zooplankton communities being

dominated by large species. The addition of nitrogen and phosphorus caused phytoplankton species composition changes and associated decreases in water clarity. These changes may be because some species of phytoplankton in the lake were nutrient limited. Since nitrogen and phosphorus were added simultaneously it is not known which nutrient was restricting phytoplankton growth. Modifying nutrient inputs would have less of an effect on cyanobacteria dynamics than the removal of perch. In order to more fully understand the role of perch in producing cyanobacterial blooms in lakes like the Lower Karori Reservoir, a large-scale eradication is needed. The Lower Karori Reservoir would be an ideal situation for such an experiment due to its small size and contained area.

3.7 REFERENCES

- Alm, G. 1946: Reasons for the occurrence of stunted fish populations with special regard to perch. *Report from the Swedish State Institute of Freshwater Research, Drottningholm* 25.
- Attayde, J. L.; Hansson, L. A. 2001: Fish-mediated nutrient recycling and the trophic cascade in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1924-1931.
- Baker, P. D.; Fabbro, L. D. 2002: A guide to the identification of common blue-green algae (Cyanoprokaryotes) in Australian freshwaters. *Identification Guide No. 25. 2nd edition*. Canberra, Cooperative Research Centre for Freshwater Ecology. 43p.
- Bell, T. 2002: The ecological consequences of unpalatable prey: phytoplankton response to nutrient and predator additions. *Oikos* 99: 59-68.
- Benndorf, J.; Boing, W.; Koop, J.; Neubauer, I. 2002: Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology* 47: 2282-2295.
- Biggs, B. J. F.; Kilroy, C. 2000: Stream periphyton monitoring manual. Christchurch, New Zealand, NIWA. 226 p.
- Brabrand, A.; Faafeng, B.; Nilssen, J. P. M. 1990: Relative importance of phosphorus supply to phytoplankton production: fish excretion versus external loading. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 364-372.
- Brooks, J. L.; Dodson, S. I. 1965: Predation, body size, and composition of plankton. *Science* 150: 28-35.

- Burns, C. W. 1968: The relationship between body size of filter feeding cladocera and the maximum size of particle ingested. *Limnology and Oceanography* 13: 675-678.
- Burns, C. W. 1998: Planktonic interactions with an austral bias: implications for biomanipulation. *Lakes and Reservoirs: Research and Management* 3: 95-104.
- Carpenter, S. R.; Kitchell, J. F.; Hodgson, J. R. 1985: Cascading trophic interactions and lake productivity. *BioScience* 35: 634-639.
- Carpenter, S. R.; Kitchell, J. F. 1993: The trophic cascade in lakes. Cambridge, Cambridge University Press. 385 p.
- Carpenter, S. R. 1996: Microcosm experiments have limited relevance for community and ecosystem ecology. *Ecology* 77: 677-680.
- Carpenter, S. R.; Caraco, N. F.; Correll, D. L.; Howarth, R. W.; Sharpley, A. N.; Smith, V. H. 1998: Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8: 559-568.
- Chapman, M. A.; Lewis, M. H. 1976: An introduction to the freshwater crustacea of New Zealand. Auckland, New Zealand, Collins. 261 p.
- Clarke, K. R.; Warwick, R. M. 2001: Change in marine communities: an approach to statistical analysis and interpretation. Plymouth, UK, PRIMER-E.
- Drenner, R. W.; Mazumder, A. 1999: Microcosm experiments have limited relevance for community and ecosystem ecology: Comment. *Ecology* 80: 1081-1085.
- Duncan, K. W. 1967: The food and population structure of perch (*Perca fluviatilis* L.) in Lake Mahinerangi. *Transactions of the Royal Society of New Zealand, Zoology* 9: 45-52.
- Entwistle, T. J.; Sonneman, J. A.; Lewis, S. H. 1997: Freshwater algae in Australia: guide to conspicuous genera. Sainty & Associates, Potts Point, Australia. 242 p.
- Flint, E. A. 1966: Toxic algae in some New Zealand freshwater ponds. *New Zealand Veterinary Journal* 14: 181-185.

- Gliwicz, Z. M.; Pijanowska, J. 1989: The role of predation in zooplankton succession. *In*: U. Sommer. *ed.* Plankton ecology: succession in plankton communities. Berlin, Springer-Verlag. 253-296
- Gliwicz, Z. M. 1990: Why do cladocerans fail to control algal blooms? *Hydrobiologia* 200/201: 83-97.
- Haider, S.; Naithani, V.; Viswanathan, P. N.; Kakkar, P. 2003: Cyanobacterial toxins: a growing environmental concern. *Chemosphere* 52: 1-21.
- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Christoffersen, K.; Burns, C. W. 2000: Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research* 22: 951-968.
- Leibold, M. A. 1989: Resource edibility and the effects of predators and productivity on the outcome of trophic interactions. *The American Naturalist* 134: 922-949.
- Leibold, M. A.; Chase, J. M.; Shurin, J. B.; Downing, A. L. 1997: Species turnover and the regulation of trophic structure. *Annual Review of Ecology and Systematics* 28: 467-494.
- Mazumder, A.; McQueen, D. J.; Taylor, J. P.; Lean, D. R. S. 1988: Effects of fertilization and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: large enclosure experiments. *Limnology and Oceanography* 33: 421-430.
- McQueen, D. J.; Post, J. R.; Mills, E. L. 1986: Trophic relationships in freshwater pelagic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 1571-1581.
- Moore, S. C. 2000: Photographic guide to the freshwater algae of New Zealand. Dunedin, New Zealand, Otago Regional Council il. 77 p.
- O'Dowd, D. J.; Green, P. T.; Lake, P. S. 2003: Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6: 812-817.
- Oksanen, L.; Fretwell, S. D.; Arruna, J.; Niemela, P. 1981: Exploitation ecosystems in gradients of primary productivity. *The American Naturalist* 118: 240-261.
- Persson, L.; Diehl, S.; Johansson, L.; Andersson, G.; Hamrin, S. F. 1992: Trophic interactions in temperate lake ecosystems: a test of food chain theory. *The American Naturalist* 140: 59-84.

- Peters, R. H.; Downing, J. A. 1984: Empirical analysis of zooplankton filtering and feeding rates. *Limnology and Oceanography* 29: 763-784.
- Porter, K. G. 1973: Selective grazing and differential digestion of algae by zooplankton. *Nature* 244: 179-180.
- Porter, K. G. 1977: The plant-animal interface in freshwater ecosystems. *American Scientist* 65: 159-170.
- Reynolds, C. S. 1984: The ecology of freshwater phytoplankton. Cambridge, Cambridge University Press 384 p.
- Romare, P.; Bergman, E.; Hansson, L.-A. 1999: The impact of larval and juvenile fish on zooplankton and algal dynamics. *Limnology and Oceanography* 44: 1655-1666.
- Schindler, D. W. 1974: Eutrophication and recovery in experimental lakes: implications for lake management. *Science* 184: 897-899.
- Schindler, D. W. 1978: Factors regulating phytoplankton production and standing crop in the world's freshwaters. *Limnology and Oceanography* 23: 478-486.
- Shapiro, J.; Lamarra, V.; Lynch, M. 1975: Biomanipulation: an ecosystem approach to lake restoration. In: Brezonik, P. L.; Fox, J. L. eds. Water quality management through biological control. Gainesville, University of Florida. Pp. 85-96
- Shiel, R. J. 1995: A guide to the identification of rotifers, cladocerans and copepods from Australian inland waters. Albury, NSW, Co-operative research centre for freshwater ecology. 144 p.
- Smith, V. H. 1983: Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671.
- Smyly, W. J. P. 1952: Observations on the food of the fry of perch (*Perca fluviatilis* Linn.) in Windermere. *Proceedings of the Zoological Society of London* 122: 407-416.
- Steffensen, D.; Burch, M.; Nicholson, B.; Drikas, M.; Baker, P. 1999: Management of toxic blue-green algae (cyanobacteria) in Australia. *Environmental Toxicology* 14: 183-195.
- Sterner, R. W. 1986: Herbivores direct and indirect effects on algal populations. *Science* 231: 605-607.

- Thomson, G. M. 1922: The naturalisation of animals and plants in New Zealand. London, Cambridge University Press. 607 p.
- Utermöhl, H. 1958: Zur Vervollkommung der quantitativen Phytoplankton Methodik (Towards a perfection of quantitative phytoplankton methodology). *Mitteilungen der Internationale Vereinigung für Theoretische und Angewandte Limnologie* 9: 1-38.
- Vanni, M. J.; Findlay, D. L. 1990: Trophic cascades and phytoplankton community structure. *Ecology* 71: 921-937.
- Vanni, M. J.; Layne, C. D. 1997: Nutrient recycling and herbivory as mechanisms in the "top-down" effect of fish on algae in lakes. *Ecology* 78: 21-40.
- Vanni, M. J.; Layne, C. D.; Arnott, S. E. 1997: "Top-down" trophic interactions in lakes: effects of fish on nutrient dynamics. *Ecology* 78: 1-20.
- Viner, A. B.; White, E. 1987: Phytoplankton growth. In: Viner, A. B. *ed.* Inland waters of New Zealand. Wellington, New Zealand, DSIR Bulletin 241. Pp. 191-223.
- White, T. C. R. 1978: The importance of a relative shortage of food in animal ecology. *Oecologia* 33: 71-86.
- Wood, S. A. 2005: Bloom forming and toxic cyanobacteria in New Zealand: species diversity, distribution, cyanotoxin production and accumulation of microcystins in selected freshwater organisms. Unpublished PhD thesis, Victoria University and Massey University, Wellington, New Zealand 306 p.
- Zaret, T. M.; Paine, R. T. 1973: Species introduction in a tropical lake. *Science* 182: 449-455.

4. GENERAL DISCUSSION

Research into the factors regulating primary production in freshwater lakes has led to considerable debate over the relative strengths of bottom-up and top-down forces in aquatic food webs. In New Zealand, lake food webs are generally thought to be primarily driven by bottom-up factors (e.g. Chapman & Green 1987; Chapman et al. 1985). However, more recent research has shown that in some cases top predators may have a significant effect on plankton communities (Jeppesen et al. 2000). This study sought to follow the nutrient dynamics, phytoplankton, zooplankton, and fish community in a lake known to have cyanobacterial blooms; and then determine the role of nutrient resources (bottom-up) versus cascading effects of fish consumers (top-down) in controlling cyanobacteria growth in the Lower Karori Reservoir:

- To establish a basic knowledge of the food web within the reservoir.
- To follow the chemical and biological dynamics of the reservoir for an extended period of time to observe seasonal changes associated with the cyanobacterial blooms.
- To experimentally manipulate the trophic levels of the food web to determine which factors (i.e. resources or consumers) were most significant in promoting the growth of cyanobacteria.

4.1 Whole lake monitoring

The Lower Karori Reservoir is a relatively deep, warm monomictic, mesotrophic lake. Physical and chemical characteristics of the reservoir that are known to promote cyanobacterial blooms include the development of thermal stratification, moderate nutrient concentrations, high water temperatures, and pH levels > 6. In particular, the low levels of nitrogen observed in the Lower Karori Reservoir probably favour nitrogen fixing cyanobacteria over other phytoplankton. Large, heavy phytoplankton taxa settle rapidly out of the water column during thermal stratification whereas buoyant species, such as cyanobacteria can alter their position in the water column to achieve the best possible conditions for nutritional and photosynthetic requirements (Reynolds et al. 1987). It has been hypothesized that cyanobacteria also have optimal physiology and growth at high temperatures. However, since high temperatures are often associated with thermal stratification the effects of temperature can become confounded.

Despite the fact that perch are not obligate planktivores, perch are likely to be having a significant effect on zooplankton populations in the Lower Karori Reservoir. The netting survey indicated that the perch population was dominated by small sized individuals. Most of the fish caught were between 60 and 110 mm. A few individuals were larger than this size but were still smaller than the maximum size reached by perch in other areas of New Zealand (Jellyman 1980). The fact that few large perch were caught is probably not due to a sampling effect given the range of mesh sizes of the gill net used, which were capable of catching much larger fish. Probable reasons for the stunted perch population include the lack of predation on the perch population and high intraspecific competition that results in low growth rates. Additionally, it is possible that perch deaths associated with cyanobacterial blooms in recent years may have killed off most of the adult perch population. The diet composition of the small fish consisted of both zooplankton and benthic macroinvertebrates, when seasonally available. Zooplankton taxa that made up a high proportion of the diet, such as *Daphnia carinata* and *Ceriodaphnia dubia*, were always at extremely low levels in the lake indicating that predation pressure on the zooplankton community may be high, despite the fact that the juvenile perch did not feed exclusively on zooplankton. These larger species of zooplankton are able to consume a wider size range and morphology of phytoplankton and are thus more likely to control phytoplankton blooms. The taxa that dominated the zooplankton community were smaller species that are probably unable to consume most of the phytoplankton taxa, such as cyanobacteria, present in the Lower Karori Reservoir.

4.2 Food web manipulation

The major result from the field manipulation experiment was that cyanobacteria levels were highest in the treatments with only the addition of perch. Densities of cyanobacteria increased dramatically after juvenile perch were added to the enclosures. Interestingly, cyanobacteria concentrations were lower in the perch and nutrient treatments than the treatment with only perch, but still had higher densities than in the nutrient only treatments. This result suggests that the nitrogen fixing *Anabaena* could have lost some competitive advantage over the other phytoplankton taxa with the addition of nitrogen. The results from this experiment should be backed up by large scale experiments, such as a whole-lake, long-term eradication of perch. Enclosure studies may not adequately reflect trophic interactions due to spatial and temporal restraints. However, this experiment was still a useful indicator of possible interactions and was

adequately long enough to witness major events in the seasonal succession of temperate planktonic communities (Brett & Goldman 1997).

While there were no differences in total zooplankton and phytoplankton abundance under any of the experimental treatments, there were changes in species composition. The control treatment was dominated by large species of both zooplankton and phytoplankton and had the greatest water clarity. Cyanobacteria densities were also lowest in the control treatment. The addition of nutrients caused a shift towards species with high chlorophyll *a* content and had the lowest water clarity. The plankton community under the perch treatment was composed of small zooplankton taxa, in particular rotifers, and had the highest levels of cyanobacteria.

The trophic cascade model predicts that a decrease in the abundance of zooplanktivorous fish will mean an increase in large zooplankton taxa and a subsequent decrease in phytoplankton biomass (Carpenter et al. 1985). However, this original model did not incorporate nutrient recycling by the zooplanktivorous fish, which can be an important source of nutrients for phytoplankton (Attayde & Hansson 2001; Vanni et al. 1997). The suitability of cyanobacteria as a food source for large zooplankton is limited due to possible toxic effects (Christoffersen & Burns 2000) and the difficulty in consuming large colonies (de Bernardi & Giussani 1990). As a result, the “top-down” effects of perch on cyanobacteria could have been due to nutrient recycling rather than reducing grazing pressure by zooplankton. Since zooplankton grazing pressure was not directly measured in this study it is not known whether perch promoted cyanobacteria growth by nutrient recycling or by reducing the abundance of large filter feeding zooplankton.

4.3 The success of biomanipulation

The trophic cascade model formed the basis for biological manipulations (termed “biomanipulation”) of freshwater food webs to improve water quality. The model was originally based on Northern Hemisphere temperate lakes and so its application for New Zealand lakes may be limited (Burns 1998). The biomanipulation concept has received much criticism (e.g. DeMelo et al. 1992) and its success is dependent on a number of assumptions. Namely, that zooplankton must be sufficiently abundant to assert control over the phytoplankton biomass and prevent the formation of blooms. Additionally, predation by zooplanktivorous fish must be

sufficiently high to reduce the grazing pressure by zooplankton, and in order to reverse this effect it must be practical to remove the fish from the waterbody. Burns (1998) identified two factors that may limit the success of biomanipulation in New Zealand lakes; planktivory by larval fish and the occurrence of inedible phytoplankton. Most native freshwater fish species are zooplanktivorous as juveniles and may reduce the size and abundance of zooplankton. In addition a lot of the phytoplankton taxa that are responsible for water quality problems in New Zealand are large celled and thus are difficult for zooplankton to consume. If inedible species are present their ability to be controlled by biomanipulation is reduced.

4.4 Conclusions

Both thermal stratification and zooplanktivorous fish can promote cyanobacterial blooms. Stratification can favour cyanobacteria since heavier species of phytoplankton sink out of the water column while cyanobacteria can migrate to the surface due to buoyancy regulation. Zooplanktivorous fish can produce increased phytoplankton biomass by two pathways. Either indirectly by reducing grazing pressure on phytoplankton by preying upon large zooplankton taxa or directly by recycling nutrients to the phytoplankton. These two pathways were not measured in this study so it is not known by which mechanism perch promoted cyanobacteria growth. Still, these results indicate that an eradication of perch would likely cause a reduction in cyanobacteria abundance and an increase in water clarity with the plankton being dominated by both larger phytoplankton and zooplankton species.

The proposal by the Karori Wildlife Sanctuary to eradicate perch from the lower reservoir in order to improve water quality should likely be successful. Biomanipulations in deep mesotrophic lakes can cause sustained phytoplankton biomass reductions (Benndorf et al. 2002). One important factor in the success of biomanipulation is the promotion of large bodied zooplankton; in particular *Daphnia* spp. (Reynolds 1994). *Daphnia carinata* is cited as one of the largest and most efficient filter-feeding zooplankton taxa in Australasia (Smirnov & Timms 1983). *Daphnia carinata* is present but occurred at low densities in the Lower Karori Reservoir. The food web manipulation experiment indicated that a removal of perch may allow *D. carinata* to build up large populations that could effectively filter phytoplankton rapidly from the water column. Even though some of the phytoplankton

community may be outside the grazing capacity of even the largest zooplankton, the large forms in this study were shown to be associated with increased water clarity.

Grazing pressure and nutrient limitation varies seasonally. The outcomes of this study may have been different if it had been conducted in another time of the year. However, cyanobacteria abundance was promoted with the addition of perch even when ambient cyanobacterial densities were low within the lake. Only phosphorus concentrations fluctuated seasonally and were lowest during stratification. Total nitrogen levels were low during the entire sampling period and did not vary a great deal. These low nitrogen levels may indicate nitrogen limitation and thus advantage nitrogen fixing cyanobacteria, which then become dominant during water column stability.

4.5 Future directions

This research showed that dominance by cyanobacteria in the Lower Karori Reservoir can be attributed to a number of factors including the seasonal development of thermal stratification, low nitrogen concentrations and the presence of zooplanktivorous perch. However, since this study was conducted there has been a complete shift in cyanobacteria species composition. During my research the dominant cyanobacterium was *Anabaena lemmermannii* and two other *Anabaena* species occurred at low densities. A new species of cyanobacteria, *A. planktonica*, was detected at the end of summer 2004 and remained at low levels for the rest of the sampling period. In November of the same year, a monospecific bloom of *A. planktonica* occurred in the reservoir (Wood 2005). There has been a change in cyanobacterial species composition and dominance over a very short time period. The consequence of this change in species on management strategies is unknown since there is little information on its ecology and physical requirements. The occurrence of this species during the cooler months could indicate that bloom formation may arise earlier and for extended periods of time.

Should management authorities desire it, the eradication of perch from the Lower Karori Reservoir should be relatively straight forward. The waterbody is small and in an enclosed area. While native fish are present, species are probably not at high abundances and none were caught during netting surveys. Restocking the reservoir with natives is a potential option after the removal of perch but species selection is critical. For example, juveniles of *Gobiomorphus* spp.

are planktivorous and can occur at extremely high densities (Burns 1998). Their predation on zooplankton populations could limit the grazing potential of the zooplankton community to control phytoplankton biomass. In order to fully understand the role of perch in promoting cyanobacterial growth, whole-lake eradication within the catchment is required, which would aid in our understanding of cyanobacterial blooms and food web dynamics within New Zealand. In addition, ensuring thermal stratification does not occur may help reduce cyanobacterial blooms, for example, using aeration tubes to promote homothermous conditions (Cooke et al. 1993). This method however, can be expensive to install and run.

4.6 REFERENCES

- Attayde, J. L.; Hansson, L. A. 2001: Fish-mediated nutrient recycling and the trophic cascade in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 1924-1931.
- Benndorf, J.; Boing, W.; Koop, J.; Neubauer, I. 2002: Top-down control of phytoplankton: the role of time scale, lake depth and trophic state. *Freshwater Biology* 47: 2282-2295.
- Brett, M. T.; Goldman, C. R. 1997: Consumer versus resource control in freshwater pelagic food webs. *Science* 275: 384-386.
- Burns, C. W. 1998: Planktonic interactions with an austral bias: implications for biomanipulation. *Lakes and Reservoirs: Research and Management* 3: 95-104.
- Carpenter, S. R.; Kitchell, J. F.; Hodgson, J. R. 1985: Cascading trophic interactions and lake productivity. *BioScience* 35: 634-639.
- Chapman, M. A.; Green, J. D. 1987: Zooplankton ecology. In: Viner, A. B. ed. Inland waters of New Zealand. Wellington, New Zealand, DSIR Bulletin 241. Pp. 225-263.
- Chapman, M. A.; Green, J. D.; Jolly, V. H. 1985: Relationships between zooplankton abundance and trophic state in seven New Zealand lakes. *Hydrobiologia* 123: 119-136.
- Christoffersen, K.; Burns, C. W. 2000: Toxic cyanobacteria in New Zealand lakes and toxicity to indigenous zooplankton. *Verhandlungen der internationalen Vereinigung für theoretische und angewandte Limnologie* 27: 3222-3225.

- Cooke, G. D.; Welch, E. B.; Peterson, S. A.; Newroth, P. R. 1993: Restoration and management of lakes and reservoirs. *2nd*, Lewis Publishers, Florida. 543 p.
- de Bernardi, R.; Giussani, G. 1990: Are blue-green algae a suitable food for zooplankton? An overview. *Hydrobiologia* 200/201: 29-41.
- DeMelo, R.; France, R.; McQueen, D. J. 1992: Biomanipulation: hit or myth? *Limnology and Oceanography* 37: 192-207.
- Jellyman, D. J. 1980: Age, growth, and reproduction of perch, *Perca fluviatilis* L., in Lake Pounui. *New Zealand Journal of Marine and Freshwater Research* 14: 391-400.
- Jeppesen, E.; Lauridsen, T.; Mitchell, S. F.; Christoffersen, K.; Burns, C. W. 2000: Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *Journal of Plankton Research* 22: 951-968.
- Reynolds, C. S.; Oliver, R. L.; Walsby, A. E. 1987: Cyanobacterial dominance: the role of buoyancy regulation in dynamic lake environments. *New Zealand Journal of Marine and Freshwater Research* 21: 379-390.
- Reynolds, C. S. 1994: The ecological basis for the successful biomanipulation of aquatic communities. *Archiv für Hydrobiologie* 130: 1-33.
- Smirnov, N. N.; Timms, B. V. 1983: A revision of the Australian Cladocera (Crustacea). Records of the Australian Museum Suppl. 1, Southwood Press Pty, Sydney.
- Vanni, M. J.; Layne, C. D.; Arnott, S. E. 1997: "Top-down" trophic interactions in lakes: effects of fish on nutrient dynamics. *Ecology* 78: 1-20.
- Wood, S. A. 2005: Bloom forming and toxic cyanobacteria in New Zealand: species diversity, distribution, cyanotoxin production and accumulation of microcystins in selected freshwater organisms. Unpublished PhD thesis, Victoria University and Massey University, Wellington, New Zealand. 306 p.