Dynamics of internal nutrient loading in a eutrophic, polymictic lake (Lake Rotorua, New Zealand)

A thesis
submitted in partial fulfilment
of the requirements for the degree of

Doctor of Philosophy

at

The University of Waikato

by

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THE UNIVERSITY OF
WAIKATO
Te Whare Wānanga o Waikato

The University of Waikato
2006

Abstract

Lake Rotorua is a large (80 km^2), polymictic, eutrophic, shallow (mean depth 10.8 m) lake in central North Island, New Zealand. Blooms of cyanobacteria and occasional anoxia of bottom waters are characteristic of the water quality in the lake during summer months (Dec-Mar.). This study examines the dynamics of internal nutrient recycling processes in Lake Rotorua, including sediment nutrient release, sedimentation and resuspension, phytoplankton nutrient limitation and the relative importance of internal and external nutrient loads on influencing cyanobacteria biomass and summer bloom formation.

Sediment nutrient release rates of phosphorus (P) in Lake Rotorua were estimated from changes in bottom water P concentration during a 19-day summer stratification event in February 2003. Changes in mass of hypolimnion P due to mixing events, together with settling, inflows, diffusion and regeneration, were factored into a simple model which was used to elucidate and quantify the complex nature of phosphorus fluxes in polymictic systems. Sediment soluble reactive phosphorus (SRP) release rates reached values of up to 26.3 mg m^{-2} d^{-1} and increased during stratification, coinciding with a decline in bottom water dissolved oxygen (DO) concentrations.

Phytoplankton nutrient limitation was examined in the lake using three *in situ* incubation experiments of 4 to 6 day duration in summer 2004. Two of the incubations were conducted during stratification, and one immediately after breakdown of stratification. Samples were enriched with either ammonium (1 mg NH_4 L^{-1}), phosphate (0.1 mg PO_4 L^{-1}), or with both nutrients. A control with no nutrient addition was used for comparison. Phytoplankton responses to nutrient additions were determined at a species level from cell counts and at a community level from changes in chlorophyll *a* (chl-*a*) concentration. A simple phytoplankton growth model was applied to consider the interacting effects of P, nitrogen (N) and light limitation. Phytoplankton biomass generally responded to N plus P additions to a greater extent than with single nutrient additions alone, however, results were often not significant. Increase in community biomass was greater for P than N, and nutrient demand decreased after breakdown of stratification. Individual species responded

differently to N and P additions, suggesting co-limitation, and that management of water quality in Lake Rotorua should restrict inputs of both N and P. Model results indicate that light also plays a major role in limiting phytoplankton biomass.

Seasonal variations in sedimentation rates of total particulate matter (TPM), total phosphorus (TP), total nitrogen (TN) and chl-*a* were measured at three sites in the lake using cylindrical sediment traps. Deployment of traps at different depths at each site showed an increase in sedimentation rates of particulate inorganic material with trap depth, indicating that sediment resuspension is an important process in this lake. Resuspension was estimated to contribute up to 71 % of TPM sedimentation at the shallowest site. Net sedimentation rates across all sites, excluding resuspension fluxes, were 4.5 g m-2 d^{-1} for TPM, and 19.8, 103.7 and 42.1 mg m^{-2} d^{-1} for TP, TN and chl-*a*, respectively. Sedimentation rates of all variables were highest in summer and at the deepest sampling site. Mean net sedimentation rates of N and P were between four and nine times greater, respectively, than estimates of net retention based on a nutrient mass balance, demonstrating that internal nutrient recycling is an important process in Lake Rotorua.

Sediment release rates of SRP and NH_4 were further determined seasonally at three sites (water depth 7, 14 and 20 m) in Lake Rotorua using *in situ* benthic chamber incubations. Rates of release of SRP ranged from 2.2 to 85.6 mg P m^{-2} d^{-1} and were largely independent of DO concentration. Two phases of NH_4 release were observed in the chamber incubations; high initial rates of up to 2200 mg N m^{-2} d^{-1} in the first 12 h of deployment followed by lower rates of up to 270 mg N m^{-2} d^{-1} in the remaining 36 h of deployment. Releases of SRP and NH_4 were highest in summer and at the deepest of the three sites. High organic matter supply rates to the sediments may be important for sustaining high rates of sediment nutrient release. A nutrient budget of Lake Rotorua indicates that internal nutrient sources derived from benthic fluxes are more important than external nutrient sources to the lake.

In the final part of this thesis, a vertically resolved water quality model, DYRESM-CAEDYM, was used to assist with quantifying the relative contributions of internal and external nutrient inputs to the lake and their relative importance to cyanobacteria bloom formation. External nutrient loads were derived for 26 tributaries as well as for

groundwater and stormwater flows. The total external load is 534 t yr^{-1} for TN and 34 t yr^{-1} for TP. Other forcing inputs to the model included meteorological data collected at a station beside the lake and discharge from the only outflow, Ohau Channel. Measured rates of sediment nutrient release obtained from benthic chamber measurements, profiles of water column nutrient concentrations, surface chl-*a* concentration and temperature and dissolved oxygen loggers were used to validate output from the DYRESM-CAEDYM model. Simulations of water column temperatures and SRP and NH_4 concentrations in Lake Rotorua showed a close representation of field measurements, and captured the timing and duration of stratification events and subsequent changes in bottom water nutrient concentrations. Model simulations of different nutrient loading scenarios indicate that reductions in sediment nutrient fluxes would be more effective in reducing cyanobacterial biomass than similar reductions in catchment fluxes, due to the incidence of large sediment nutrient release events in association with summer blooms. This finding indicates that only a significant and prolonged reduction in external loads, that in turn would reduce internal loads, will ultimately decrease cyanobacteria biomass in Lake Rotorua.

In this study, field work and modelling were used to demonstrate the importance of internal nutrient loads in sustaining the current trophic status of Lake Rotorua. High external loading rates, coupled with high rates of organic matter sedimentation and sediment nutrient release rates, suggest that high phytoplankton biomass will remain a feature of this lake unless a significant and prolonged reduction in both N and P external loads is undertaken. The results of this study also emphasised the importance of conducting experimental measures of sedimentation and sediment nutrient release rates within eutrophic lakes, particularly where internal recycling processes may represent the dominant sources of nutrients to the lake.

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Acknowledgements

First and foremost, I would like to acknowledge and thank my supervisors Prof. David Hamilton and Dr Conrad Pilditch (University of Waikato) and Dr Julie Hall and Max Gibbs (NIWA), for their insights, advice and guidance throughout. I particularly thank David for his enthusiasm and mentoring over the last three years. I am also grateful to Assoc. Prof. John Green for initially instigating this project.

I wish to thank Dr. Eloise Ryan, Dudley Bell, and Alex Ring (University of Waikato), Brian Coxhead (SeaQuest Ltd), Gerald Inskeep (Eastern Region Fish and Game) and Andrew Lang (Rotorua District Council) for field and technical assistance throughout the project. Field accommodation and on-site laboratory facilities were provided by Eastern Region Fish and Game. I also thank staff and students of the Centre for Ecology and Biodiversity Research (University of Waikato) for technical support at many stages.

I thank Dr Ian Hawes for useful discussions on Chapter 3, and Craig Putt (Environment Bay of Plenty) for additional field assistance in Chapter 5. Steve Hardy, Peter Jarman and Chris Sistern (University of Waikato) provided technical support with construction of the benthic chambers and servicing of data loggers. Dr Kit Rutherford (NIWA), Prof. Warwick Silvester (University of Waikato) and Dr Ami Nishri (Israel Oceanographic and Limnological Research Institute) provided valuable discussions in relation to Chapters 4 and 5.

I would like to acknowledge Paul Dell, John McIntosh, Paul Shoals, Glenn Ellery, Matt Bloxham and John Gibbons-Davies (Environment Bay of Plenty) for provision of the lake and inflow water quality data used to validate the model in Chapter 6. I also thank Tora Uraoka, Jose Beyá and Dr Bob Spigel (NIWA) for providing assistance with aspects of the modelling and data-setup.

Throughout this work I was financially assisted by the Hillary Jolly Memorial Scholarship at the University of Waikato. The research in this thesis was financially supported by Environment Bay of Plenty. Attendance to the SIL conference in

Finland was assisted by a Royal Society of New Zealand Travel Award, and travel to the ASLO summer congress in Spain and International Symposium on Shallow Lakes in the Netherlands was fully supported by a SIL Trust fund (1987) Travel Award, through the New Zealand Freshwater Sciences Society.

Most importantly, I would like to thank my partner Marie for her unrelenting support and encouragement. I also thank my family and friends, particularly for their patience throughout the final stages.

Preface

This thesis consists of five chapters (Chapters 2-6) that describe the results of this study and have been set out as papers which have either been submitted or are intended for submission for publication in peer reviewed scientific journals. Except where referenced, the work in this thesis, including field and laboratory work, data analyses, interpretation and writing, was produced from my own ideas and work undertaken while under the supervision of Prof. David Hamilton, Dr Conrad Pilditch, Associate Professor John Green (Waikato University) and Dr Julie Hall and Max Gibbs (National Institute of Water and Atmospheric Research).

Chapter 2 has been accepted for publication by *Verhandlung Internationale Vereingung de Limnologie* (29) under the title "Sediment phosphorus release during stratification in polymictic Lake Rotorua, New Zealand" by D. F. Burger, D. P. Hamilton, C. A. Pilditch, M. M. Gibbs and J. A. Hall.

Chapter 3 has been prepared for submission to *Journal of Plankton Research* as "Nutrient limitation of phytoplankton populations in polymictic Lake Rotorua, New Zealand: Different responses of communities and species", by D. F. Burger, D. P. Hamilton, J. A. Hall and E. F. Ryan.

Chapter 4 is intended for submission to *New Zealand Journal of Marine and Freshwater Research* under the title of "Phosphorus and nitrogen sedimentation in Lake Rotorua, New Zealand", by D. F. Burger, D. P. Hamilton, M. M. Gibbs and C. A. Pilditch.

Chapter 5, "Benthic nutrient fluxes in a eutrophic, polymictic lake", by D. F. Burger, D. P. Hamilton, C. A. Pilditch, and M. M. Gibbs, has been accepted for publication in *Hydrobiologia* as part of the published proceedings from the 5th International Symposium on Shallow Lakes (The Netherlands, June 2005).

Chapter 6 has been prepared for submission to an applied aquatic ecology journal. It is entitled "External versus internal nitrogen and phosphorus loads on phytoplankton biomass in a eutrophic, polymictic lake" by D. F. Burger, D. P. Hamilton and C. A. Pilditch.

Chapter 1: General introduction

1.1 Motivation

Over recent decades, anthropogenic discharges of nutrients to aquatic systems has accelerated eutrophication in many lakes throughout the world (Wetzel, 1992). Eutrophication has been particularly evident in shallow lake systems where elevated water column concentrations of nitrogen (N) and phosphorus (P), derived from point source discharges, have often led to the formation and persistence of large and potentially toxic cyanobacteria blooms (Marsden, 1989; Scheffer, 1997). Additionally, greater rates of primary production have increased rates of organic matter deposition to the benthos, which may result in deoxygenation of bottom waters during stratification, potentially enhancing resupply of nutrients to the water column from the bottom sediments (Nürnberg, 1987; Boström et al., 1988; Søndergaard et al., 2003).

High rates of internal nutrient loading have delayed the recovery of many eutrophic lakes, even after substantial reductions in external nutrient loading from point-source discharges (Søndergaard et al., 1999; Phillips et al., 2005; Jeppesen et al., 2005). Studies of lake nutrient cycling, particularly in Northern Hemisphere lakes, emphasise P release because of its impact on phytoplankton production (e.g., OECD, 1982; Kleeberg and Kozerski, 1997). However, N can also limit or co-limit phytoplankton growth (Philips et al., 1997; Hameed et al., 1999) with substantial evidence of N limitation in New Zealand volcanic lakes (White and Payne, 1978; Vincent, 1984; White et al., 1986).

Eutrophication due to high external nutrient loads have also impacted many lakes in New Zealand (Vincent et al., 1984; Rutherford et al., 1996; Vant and Gilliland, 1991), and research and management has focused primarily on controlling catchment nutrient loads (e.g. Hoare, 1987; Vant, 1987). Only a few studies (e.g. Priscu et al., 1986) have examined the magnitude and significance of internal loading. The objective of this thesis is to examine the dynamics and temporal and spatial variability of sediment nutrient fluxes, phytoplankton nutrient limitation and external

versus internal nutrient loads on cyanobacteria biomass. This study is focused on Lake Rotorua, however, insights presented in this research also have important implications for the management of other eutrophic lakes in New Zealand and internationally.

1.2 Overview of Lake Rotorua

Lake Rotorua is the largest (area 79 km^2) of 14 lakes situated in the Rotorua Lakes district, Central North Island, New Zealand. The Rotorua district is important not only for recreational, aesthetic and cultural values, but also for tourism, supporting over 1.2 million visitors each year and representing approximately $260 million dollars of added value to the local economy (Bell et al., 2004).

Lake Rotorua is a polymictic, shallow (mean depth 10.8 m), volcanic lake formed approximately 210,000 years ago as a result of an eruption in the Mamaku region, and collapse of the Rotorua caldera (Healy, 1975; White et al., 2004). The surrounding area consists of ignimbrite and large rhyolite extrusions, which also forms Mokoia Island near the centre of the lake. Lake Rotorua is situated adjacent to two geothermal fields; the large (area 18-28 km^2) Rotorua field beneath Rotorua City at the southern margins of the lake and the Tikitere field, situated north-west of the lake (Gordon et al., 2001; White et al., 2004). Natural discharges of chloride and acid sulphate geothermal waters occur as small inflows or springs at the lake edge (McColl, 1975).

The catchment of Lake Rotorua (area 425 km^2) is dominated by agriculture (48 %) and exotic forestry (23 %), and is drained by nine major inflows (Hoare, 1980b). Like many shallow lake systems, Lake Rotorua has a long history of high external nutrient loading (Fish, 1975; Hoare, 1987; Rutherford et al., 1989; Rutherford, 2004), including discharges of treated sewage from Rotorua City (population 60,000) between 1973 and 1991 (Hoare, 1980a; Rutherford et al., 1996). Internal nutrient loads are also thought to represent a substantial portion of the total lake nutrient load (Fish, 1975; Rutherford et al., 1996), particularly in association with summer stratification events and rapid reductions in bottom-water concentrations of dissolved oxygen.

Management solutions to improve the water quality of Lake Rotorua have focused largely on reducing external nutrient loads to the lake. However, the lake has become increasingly eutrophic (Rutherford et al., 1996) and prolific cyanobacteria blooms remain a feature of the lake over the summer months. An independent report to the New Zealand Ministry for the Environment (Hamilton, 2003) to evaluate short-term management options for lakes Rotorua and Rotoiti identified several fundamental research needs that are critical to improved management of the two lakes. For Lake Rotorua, these include (1) better understanding of the dynamics and succession of phytoplankton blooms, (2) quantification and understanding of the size and role of internal nutrient loads, and (3) more accurate characterisation of external nutrient inputs. The first two of these needs are addressed directly in this thesis, while the third is a direct outcome arising from detailed work on the nutrient dynamics of the lake.

1.3 Thesis overview

This thesis comprises five research chapters (Chapters 2-6) written as independent scientific papers which form a logical progression for examination and understanding of the nutrient dynamics of Lake Rotorua. The final chapter (Chapter 7) presents the conclusions arising from the research and makes recommendations for future work.

In Chapter 2, sediment release rates of phosphorus to the overlying water column in Lake Rotorua were estimated from changes in bottom water phosphorus concentration during a summer stratification event. Changes in mass of hypolimnion P due to mixing events, as well as settling, inflows, diffusion and regeneration, were accounted for in a simple model which was used to elucidate and quantify the complex nature of phosphorus fluxes in polymictic systems.

In Chapter 3, phytoplankton nutrient limitation was examined in Lake Rotorua using three *in situ* incubation experiments conducted in summer. Phytoplankton responses to additions of bioavailable P, N or both P and N were determined at a community level from changes in chlorophyll *a* concentration, and at a species level from cell counts. A simple phytoplankton growth model was applied to examine the interacting effects of P, N and light limitation at two incubation depths.

In Chapter 4, spatial and temporal variations in sedimentation rates of total particulate matter (TPM), particulate P, particulate N and chlorophyll *a* were examined to better understand the internal nutrient recycling process in Lake Rotorua. Sedimentation rates were measured using sediment traps deployed at several depths in the water column at each site. Gross rates of sedimentation were corrected for resuspension due to the dominance or resuspension processes in the shallower regions of the lake associated with wave action which may resuspend bottom sediments, as well as for the pelagic zone due to horizontal transport processes.

To assess the magnitude of internal nutrient loads from the sediments in Lake Rotorua, sediment release rates of soluble reactive phosphorus (SRP) and ammonium (NH_4) were determined seasonally at three sites in Chapter 5 using *in situ* light and dark benthic chamber deployments. Sites were chosen to reflect the natural variability in mixing regime, from permanently well-mixed and oxygenated conditions in the shallow regions to periodically stratified and anoxic conditions in the deeper regions of the lake. Incubations were conducted over 48 hours to create anoxic conditions in the chambers at the deeper lake sites (depth 14 and 20 m), to examine the importance of dissolved oxygen concentrations on release rates. Nutrient release rates at the three sites were compared to mean daily inputs of external nutrients to the lake to determine the magnitude of internal loading.

To examine the hypothesis that sediment nutrient fluxes are at least as important as external loads for maintaining high water column nutrient concentrations and phytoplankton biomass in Lake Rotorua, a coupled hydrodynamic-ecological model was applied in Chapter 6 to simulate internal and external loading rates in the lake. Model simulations were validated over a three-year period against field data, using comparisons of temperature and concentrations of dissolved oxygen, nutrients and chlorophyll *a*. Potential management scenarios of external versus internal load reductions on water column nutrient concentrations and cyanobacterial biomass were simulated with the calibrated model. Mean annual external nutrient loads were also accurately determined to examine the relative importance of point-source nutrient inputs to the lake.

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Chapter 2: Sediment phosphorus release during stratification in polymictic Lake Rotorua, New Zealand[1]

2.1 Introduction

Nutrients released across the sediment-water interface during stratification and deoxygenation events may contribute a significant fraction of the total nutrient requirements for primary production in shallow lakes. In eutrophic lakes, internal nutrient cycling may sustain high nutrient concentrations regardless of external nutrient load reductions (Marsden, 1989; Anderson and Ring, 1999). For example, in eutrophic Lake Rotorua, New Zealand, there has been little change in nutrient concentrations and trophic status over the last two decades despite sewage diversion in 1991 (Burns et al., 1997). Previous predictions of water quality in this lake indicate that internal nutrient loads and subsequent fluxes across the sediment-water interface are likely to be a significant component of the total nutrient budget (Rutherford et al., 1996). Our objective was to quantify sediment phosphorus release in polymictic Lake Rotorua during a stratification event.

Nutrient release rates may be determined from annual nutrient budgets, experimentally from benthic chambers or sediment cores, or from observed increases in hypolimnion nutrient concentrations during summer stratification (Nürnberg, 1998). However, release rates may be difficult to quantify in polymictic lakes due to high variability in the extent and duration of stratification. In this study, we estimated phosphorus (P) release rates from increases in hypolimnion P concentration, with corrections for changes in P from settling, diffusion, mixing, inflows and regeneration.

[1] Published as: D.F. Burger, D.P. Hamilton, C.A. Pilditch, M.M. Gibbs and J.A. Hall (2005): Sediment phosphorus release during stratification in Lake Rotorua, New Zealand. *Verhandlung Internationale Vereingung de Limnologie* 29: 811-814.

2.2 Methods

Lake Rotorua is a large (79.8 km^2), shallow (mean depth 10.8 m), eutrophic lake in central North Island, New Zealand (Fig. 2.1). Sampling was carried out at a central 20 m deep station (Fig. 2.1) in summer from December 2002 to March 2003. At the central lake station, temperature loggers (ODYSSEY, Dataflow Systems Ltd) were deployed at 2 m depth intervals and set to record every 10 minutes. Dissolved oxygen concentration in the hypolimnion was determined using either a Seabird Electronics (SBE) 19-plus Seacat Profiler or a YSI Instruments 6000 logger. Water samples were collected at 1- to 5-day intervals during stratified periods from the surface-mixed layer (depth integrated sample 0-8 m) and from three discrete depths beneath the thermocline (12, 15.5 and 19 m) to quantify changes in nutrient concentrations. Climate data (wind speed and direction, rainfall and light) were obtained from Rotorua Airport adjacent to the lake (Fig. 2.1).

Water samples were analysed for dissolved reactive phosphorus (SRP) concentration by filtration (Whatman filters, nominal pore size 1μm) and spectrophotometric analysis on a Lachat Instruments flow injection analyser (FIA). Total phosphorus (TP) concentrations were determined on unfiltered samples with a modified peroxodisulphate digestion followed by analysis on the FIA as for SRP (Ebina et al., 1983).

2.2.1 Nutrient Release Calculations

During a prolonged period of stratification, we divided the lake into horizontal 1-m layers, with the volume of each layer determined from the lake hypsographic curve. SRP and TP concentrations in each layer were determined by interpolation of measured values (0-8, 12, 15.5 and 20 m), and multiplied by volume to give layer nutrient mass. Thermocline depth (m) was given by $\partial T/\partial z$ = minimum (e.g. Hoare and Spigel, 1987), where z is water depth and T is water temperature (°C). This was then used to calculate thermocline planar surface area (A_S, m^2) and sediment surface area below the thermocline (A_{Sed}, m^2). Total mass of SRP and TP in the hypolimnion and epilimnion were calculated from the thermocline depth. SRP and TP release rates (R_{SRP} and R_{TP}, mg m^{-2} day^{-1}) for sediments in the hypolimnion were calculated as follows:

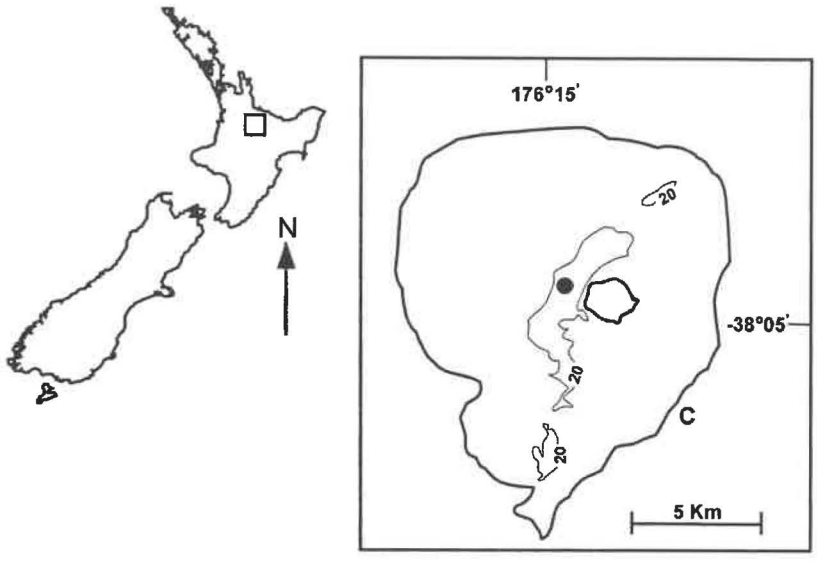

Figure 2.1: Map of Lake Rotorua showing the location of the sampling station (•), adjacent to Mokoia Island, the 20-m depth contour and the climate station (C).

$$R_{SRP}(t) = \frac{M(t-1) - M(t) - Mix - Q - D' - R'}{A_{Sed}} \tag{2.1}$$

$$R_{TP}(t) = \frac{M(t-1) - M(t) - \omega - Mix - Q - D' - R'}{A_{Sed}} \tag{2.2}$$

where M is hypolimnion mass of SRP or TP, t is day of stratification and *Mix*, Q, D', R' and ω is mass lost or gained due to mixing, plunging inflows, diffusion, regeneration and settling, respectively. Changes in mass due to mixing (*Mix*) were calculated daily from the change in thermocline depth. One cold-water spring (Hamurana) was included as an inflow to the hypolimnion using mean base flow SRP and TP concentrations and discharge rates (Rutherford, 2003).

Diffusion across the thermocline was calculated according to the concentration gradient (MacIntyre et al., 1999) and was quantified using a lake-wide average of the vertical eddy diffusion coefficient (K_z) as defined by Yeates and Imberger (2004):

$$\overline{K}_z(z) = \frac{200N^2(z)}{L_N N^2_{\max}} K_M \tag{2.3}$$

where K_M is the molecular heat diffusion coefficient and N^2 the Brunt-Vaisala buoyancy frequency, defined by:

$$N^2 = (-g/\rho)(\partial\rho/\partial z) \tag{2.4}$$

where g is gravity (9.81m s^{-2}) and ρ density (Spigel and Imberger 1987). Lake number (Ln, dimensionless, Imberger and Patterson, 1990) was defined as:

$$Ln = \frac{gS_t(1 - z_T/z_m)}{\rho_0 u_*^2 (1 - z_g/z_m)} \tag{2.5}$$

where z_T is the height of the thermocline (m), z_g the height of the centre of volume (m), u_* the surface shear velocity due to surface wind stress (m s^{-1}), ρ_S the surface water density and S_t the Schmidt stability parameter defined as:

$$S_t = \int_0^{z_m} (z - z_g) A(z) \rho(z) dz \tag{2.6}$$

u_* was calculated according to Spigel and Imberger (1987):

$$u_* = \left[(\rho_{Air}\rho_0 - 1) C_D U^2\right]^{0.5} \tag{2.7}$$

where ρ_{Air} is the density of air (1.2 kg m^{-3}), ρ_0 is the average density of water (1000 kg m^{-3}), C_D the neutral drag coefficient (1.3 10^3) and U the daily average wind speed (m s^{-1}).

Regeneration rates were taken as the relative aerobic phosphorus mineralisation rate from Robson and Hamilton (2004). Settling rate was assigned a negative value (-0.03 m day^{-1}) due to the dominance of highly buoyant cyanobacterial populations (*Anabaena* sp. and *Microcystis* sp., collectively > 10,000 cells mL^{-1}) in the surface-mixed layer, which produced TP concentrations in the epilimnion which were strongly elevated over those of the hypolimnion during the period of interest.

2.3 Results

Lake Rotorua was stratified for 19 days from 1 February 2003. The maximum water column temperature gradient was 2.5 °C and the thermocline depth was generally between 4 and 12 m (Fig. 2.2). Dissolved oxygen concentration in the hypolimnion declined to < 1 mg L^{-1} by the end of the stratified period but with occasional increases due to partial water column mixing events. During stratification, SRP and TP concentrations in the hypolimnion increased from 0.02 to 0.08 mg L^{-1} (Fig. 2.3) and 0.04 to 0.12 mg L^{-1}, respectively.

The estimated sediment SRP release rates increased from 0.88 to 13.80 mg m^{-2} day^{-1} on days 4 and 19 respectively, coinciding with a general decrease in dissolved oxygen (Fig. 2.4). Release rates of TP were 8.8 and 26.3 mg m^{-2} day^{-1} for these two days (Fig. 2.4). SRP and TP release rates were significantly correlated ($p < 0.05$) with dissolved oxygen concentration (Pearson's correlation coefficient, $r = 0.92$ and 0.90, respectively).

A sensitivity analysis was conducted on the parameter values for P settling and regeneration. Sedimentation rates were varied from -0.1 to 0.03 m day^{-1} to reflect possible variations due to typical P sedimentation rates in lakes (Chapra, 1997) or buoyant particulate P associated with presence of cyanobacteria. TP release rates ranged from 12.3 to 29.4 and 5.8 to 23.6 mg m^{-2} day^{-1} when assigned sedimentation rates of -0.1 and 0.03 m day^{-1}, respectively. Decreasing the regeneration rate for SRP from 0.05 to 0.03 day^{-1} increased the release rates of range 0.9 to13.8 mg m^{-2} day^{-1} to a new range of 1.5 to 16.6 mg m^{-2} day^{-1}.

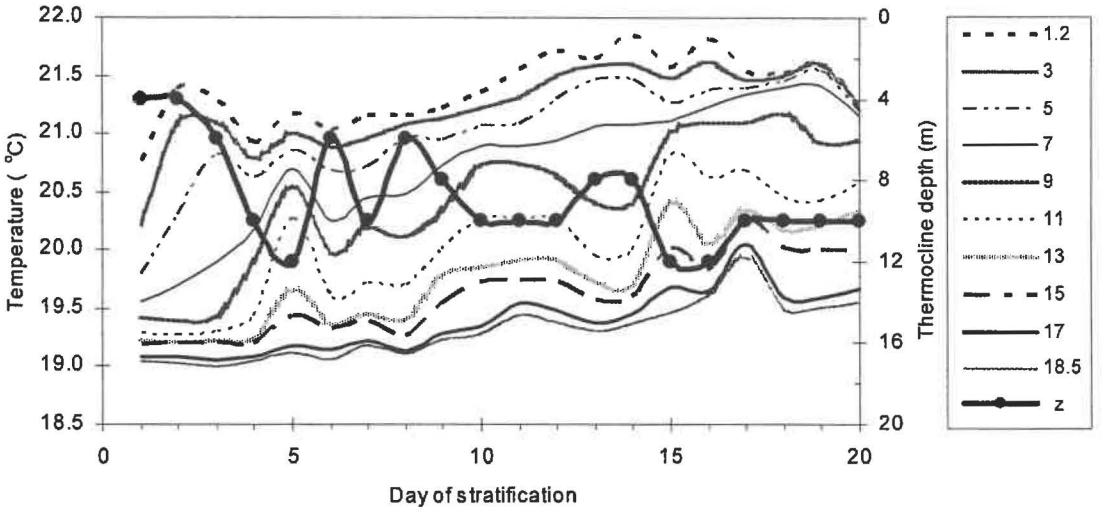

Figure 2.2: Temperature (1.2 to 18.5 m depths) and thermocline depth (*z*), Lake Rotorua, 1-19 Feb. 2003.

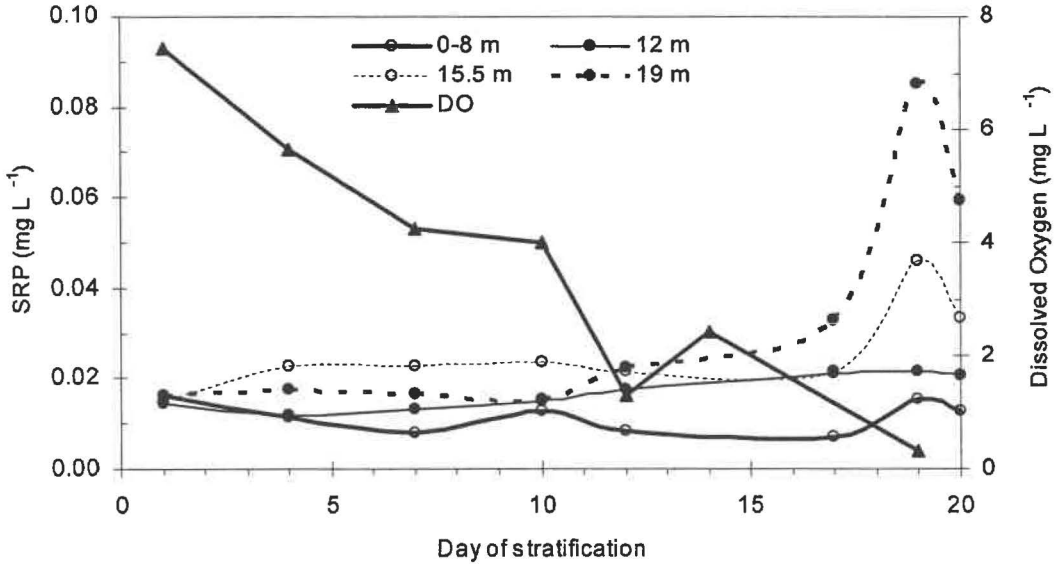

Figure 2.3: Water column soluble reactive phosphorus (SRP) and hypolimnion dissolved oxygen concentration (DO, depth 19 m), Lake Rotorua, 1-19 Feb. 2003.

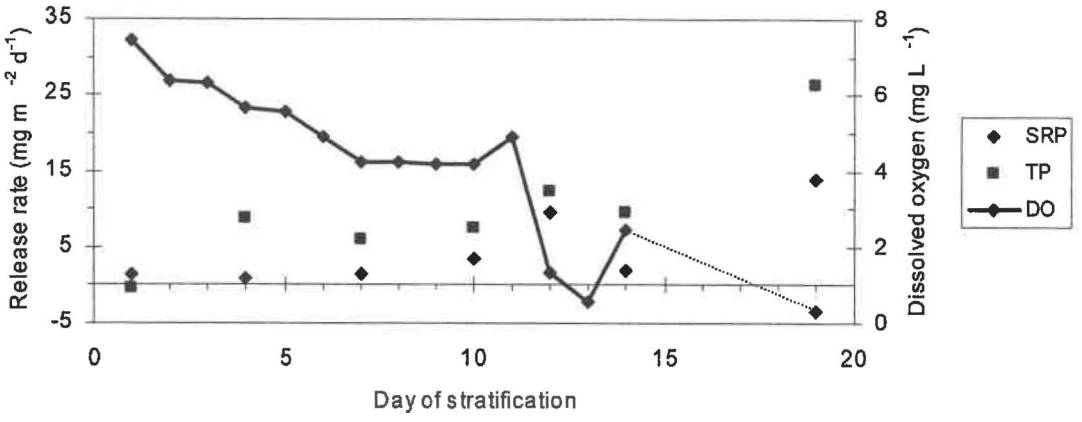

Figure 2.4: Sediment soluble reactive phosphorus (SRP) and total phosphorus (TP) release rates and hypolimnion dissolved oxygen concentration during a stratification event, 1-19 Feb. 2003.

2.4 Discussion

Our results demonstrate a clear increase in sediment P release rates following a decline in dissolved oxygen concentration during a stratification event in polymictic Lake Rotorua. The method used to determine release rates from bottom sediments is well suited to polymictic lakes where incomplete mixing and re-stratification complicate the ideal case of the hypolimnion being isolated from P transfers to and from the epilimnion. Changes in mass of hypolimnion P due to mixing, settling, inflows, diffusion and regeneration are accurately accounted for in this model. The P release rates calculated for Lake Rotorua are similar to those of shallow eutrophic lakes elsewhere (e.g. Anderson and Ring, 1999; Penn et al., 2000).

Phosphorus release rates represent an average for the whole sediment surface area under the thermocline, but rates could be expected to vary locally within the hypolimnion. Preliminary results of SRP release from *in situ* benthic chamber deployments at our 20 m deep site were up to 50 mg m^{-2} day^{-1} during anoxia, although much lower at shallower sites. Fluxes calculated from our phosphorus budget for the hypolimnion appear to be at intermediate levels amongst the range that has been measured experimentally with chambers.

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Chapter 3: Nutrient limitation of phytoplankton populations in Lake Rotorua: Different responses of communities and species[1]

Abstract

Phytoplankton nutrient limitation was examined in Lake Rotorua using three *in situ* incubation experiments of 4 to 6 days duration in summer 2004. Two of the incubations were conducted during stratification, and one immediately after breakdown of stratification. Samples were enriched with ammonium (1 mg NH_4 L^{-1}), phosphate (0.1 mg PO_4 L^{-1}) or with both nutrients. A control containing no added nutrients was used for comparison. Phytoplankton responses to nutrient additions were determined at a species level from cell counts and at a community level from changes in chlorophyll *a* concentration. A simple phytoplankton growth model was applied to consider the interacting effects of phosphorus (P), nitrogen (N) and light limitation. Phytoplankton biomass generally responded to N plus P additions to a greater extent than with single nutrient additions, though results were often not significant. Increase in community biomass was greater for P than N, and nutrient demand decreased after breakdown of stratification. Individual species responded differently to N and P additions, suggesting co-limitation, and that management of water quality in Lake Rotorua should restrict inputs of both N and P. Model results indicate that light also plays a major role in regulating phytoplankton biomass.

3.1 Introduction

Liebigs 'Law of the Minimum' provides a theoretical basis on which many lake management strategies have been predicted. The classical paradigm, based mostly on results from Northern Hemisphere lakes, is that phosphorus (P) is the nutrient that most commonly limits phytoplankton growth (Hecky and Kilham, 1988), hence the widespread application of the 'Vollenweider model' (OECD, 1982) to predict

[1] To be submitted to *Journal of Plankton Research* as "Nutrient limitation of phytoplankton populations in polymictic Lake Rotorua, New Zealand: Different responses of communities and species", by D. F. Burger, D. P. Hamilton, J. A. Hall and E. F. Ryan.

chlorophyll *a* (chl-*a*) concentrations in lakes. Other nutrients, including nitrogen (N), silica, and micronutrients can also limit or co-limit phytoplankton growth (White et al., 1986; Phlips et al., 1997; Hameed et al., 1999) and limitation by N is considered to be as prevalent as limitation by P (Elser et al., 1990).

Evidence of nutrient limitation may be ascertained by a combination of water column or seston elemental ratios, nutrient bioassay experiments and short-term physiological experiments (see Hecky and Kilham, 1988; Wood and Oliver, 1995; Beardall et al., 2001a). Elemental composition is often used to approximate which nutrient is most likely to limit growth, based on the Redfield molar ratio of 106 C: 16 N: 1 P (Redfield, 1958). However, ratios are often highly variable (Falkowski, 2000) and seston analysis is prone to contamination from bacteria, zooplankton and other non-algal organic and inorganic material (Beardall et al., 2001a).

Algal bioassay experiments compare changes in total community biomass or productivity of lake water samples with no added nutrients against treatments with added nutrients or macronutrients. Samples are typically incubated under highly regulated light and temperature regimes in the laboratory (e.g., White et al., 1986; Philips et al., 1997), although *in situ* bottle incubations (e.g., Dodds et al., 1993; Levine et al., 1997) and mesocosms (Levine and Schindler, 1999) have also been used. An increase in biomass or nutrient uptake in enriched treatments, compared with controls, is used as an indicator of nutrient deficiency (Healey, 1979).

Results of bioassay experiments may be influenced by alterations in the normal physical, chemical or biological environment experienced by phytoplankton (Elser et al., 1990). Nutrient re-supply is neglected in the enclosed experimental environment (Healey, 1979), and there is generally reduced turbulence (Levine et al., 1997) and zooplankton grazing, while water chemistry is altered by filtering lake water added to bioassays (Wood and Oliver, 1995). Light limitation may also be reduced when samples are incubated in the laboratory under a controlled light regime (Beardall et al., 2001a). Enclosures therefore often produce a change in species composition compared with natural samples (Levine et al., 1997; Beardall et al., 2001a).

Nutrient bioassays have focused mostly on measurements of phytoplankton community biomass, often approximated from chl-*a* concentration, as opposed to individual species' responses (Hecky and Kilham, 1988). Cellular chl-*a* concentration differs between species, and responses to nutrient additions are also species-specific (Reynolds, 1997; Mitrovic et al., 2001). Furthermore, White et al. (1978) found that under N limiting conditions, N additions increase cellular chl-*a* at levels that overestimate biomass, while light limitation may also produce a similar response (Venrick, 1988; Shortreed and Stockner, 1990).

Physiological measurements of nutrient limitation have in some cases been used in conjunction with growth bioassays. Assays of phytoplankton alkaline phosphatase activity and luxury phosphorus accumulation have been used as measures of P limitation (e.g., Rose and Axler, 1998; Hameed et al., 1999; Steinhart et al., 2002) and ammonium accumulation, transport capacity and enhancement as measures of N deficiency (e.g., Vincent 1984; Hameed et al., 1999). Nutrient induced fluorescence transients have also been used to provide near real time differentiation of N and P limitation (e.g., Wood and Oliver, 1995; Beardall et al., 2001b). There are many problems associated with the use and interpretation of physiological assays (see reviews by Wood and Oliver, 1995; Beardall et al., 2001a) and there may be inconsistencies in results between techniques (e.g., Hameed et al., 1999).

The objective of this study was to examine P and N limitation in populations of Lake Rotorua phytoplankton, with particular focus on species-specific responses to nutrient limitation. Growth bioassays were conducted *in situ* at two depths and on three occasions over summer to capture differences associated with the polymictic nature of the lake. Comparisons were made with earlier bioassay experiments (White and Payne, 1978; White et al., 1985; White et al., 1986) to test for possible changes in the limiting nutrient. A model of phytoplankton growth was also applied to examine the interacting effects of light, P and N on the phytoplankton growth in the lake.

3.1.1 Study site

Lake Rotorua is a large (79.8 km^2), shallow (mean depth 10.8 m) lake of volcanic origin in central North Island, New Zealand (Fig. 3.1). The lake stratifies intermittently, for periods of up to 3-4 weeks, during summer. Stratification events

are associated with rapid reductions in bottom-water concentrations of dissolved oxygen, and increases in soluble reactive phosphorus (SRP) (Burger et al., 2005) and ammonium (NH_4). Lake Rotorua is eutrophic (Rutherford et al., 1996) and annual mean concentrations of total phosphorus (TP) and total nitrogen (TN) are 0.055 mg L^{-1} and 0.814 mg L^{-1} respectively (Burger, unpublished data). Lake Rotorua has a catchment area of 425 km^2 which is dominated by agriculture (48 %) and plantation forestry (23 %). Nine major streams and 18 minor streams, urban drains and geothermal springs contribute approximately 536 t TN and 34 t TP to the lake annually (see Chapter 6).

There has been little change in nutrient concentrations and trophic status of Lake Rotorua, despite removal of treated wastewater inputs from Rotorua city (population 65,000) from the lake in 1991 (Burns et al., 1997). Phytoplankton nutrient limitation has previously been examined in the lake using 4 or 5-day growth incubations (White and Payne, 1978), short term physiological bioassays (Vincent, 1981; White et al., 1985) or both techniques (White et al., 1986). Chlorophyll *a* concentrations in *in situ* incubations consistently showed a positive response to nitrogen additions (White and Payne, 1978; White et al., 1986), with little change invoked by phosphate and trace

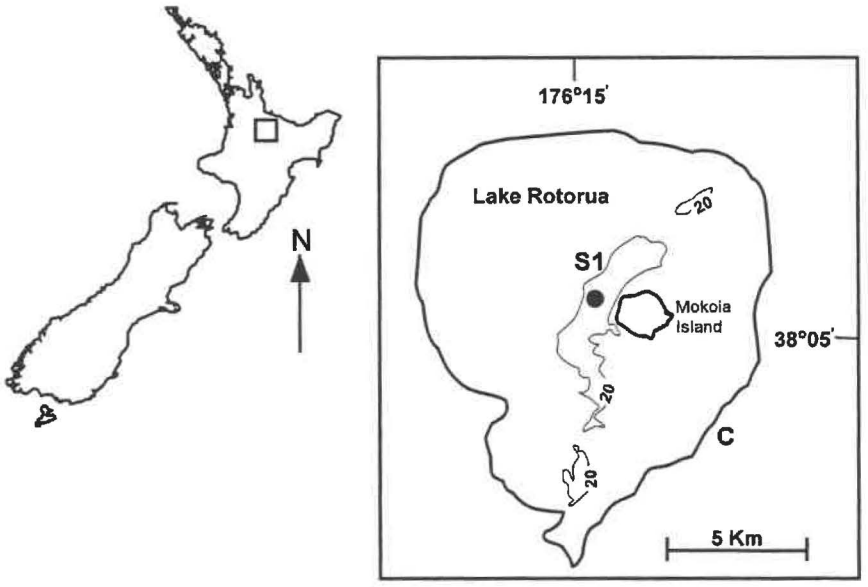

Figure 3.1: Map of Lake Rotorua showing the sampling location, Site 1(S1,•), adjacent to Mokoia Island, 20-m depth contour and climate station (C).

element additions (White and Payne, 1978). N limitation was also established by Vincent (1984) using three different bioassay techniques. White et al. (1985) suggested that limitation by P would not occur in Lake Rotorua phytoplankton populations if concentrations of dissolved reactive P were greater than 1 mg m^{-3}, and that N limitation would not occur at nitrate (NO_3) concentrations greater than 1.5 mg m^{-3}.

3.2 Methods

3.2.1 Field sampling

In situ incubations were carried out at a central lake site (site 1, depth = 20 m) for 4 or 6 days on three separate occasions (starting 23 and 30 Jan., and 9 Feb.) in summer 2004. On each occasion, 3-L PET® clear containers were filled with lake water from either 0.5 m ('surface') or 5 m depth, corresponding to the depth selected for incubating the samples. Duplicate bottles were enriched with either ammonium chloride (NH_4Cl), potassium dihydrogen phosphate (KH_2PO_4) or a combination of both nutrients, to a final concentration of 1 mg L^{-1} NH_4 and/or 0.1 mg L^{-1} PO_4. Control bottles containing no added nutrients were also incubated at both depths.

Initial (pre-incubation) water samples were collected at the two depths and preserved in Lugols iodine for subsequent phytoplankton enumeration. Additional samples were filtered through 0.45 µm membrane syringe filters and frozen for analysis of filterable nutrients (NH_4, NO_2, NO_3 and SRP) using a Lachat Instruments flow injection analyser (FIA, Zellweger Analytics, 2000). Filters were frozen for subsequent analysis of chl-*a* in duplicate, using the spectro-fluorometric method of Arar and Collins (1992). Chlorophyll *a* and cell count analyses were repeated for each bottle after the incubation period. Water column samples were also analysed for TP and TN concentrations simultaneously using a modified peroxodisulphate digestion, followed by analysis on the FIA as for SRP and NO_3 (Ebina et al., 1983). Conductivity-temperature-depth (CTD) profiles (Seabird Electronics) with additional CTD-mounted sensors for photosynthetically available radiation (PAR, Licor Ltd.), chlorophyll *a* fluorescence (Chelsea Instruments Ltd.) and dissolved oxygen (Seabird Electronics) were collected on the first and final days of each incubation.

Water column temperature used to assess stratification before and during the experiments was obtained from ODYSSEY (Dataflow Systems Ltd) temperature loggers at 2 m depth intervals at site 1. Dissolved oxygen concentrations in the bottom waters were obtained from *in situ* loggers (Greenspan Technology Ltd) deployed at 19 m, also at site 1. Temperature and dissolved oxygen were recorded every 5 and 30 minutes, respectively. Values of PAR (I, µmol quanta m^{-2} s^{-1}) at each incubation depth (z) were calculated using the Beer-Lambert equation:

$$I_z = I'_0 e^{-K_d z} \qquad (3.1)$$

where I'_0 is surface PAR intensity and K_d is the light extinction coefficient calculated from underwater PAR values derived from the CTD profiles.

3.2.2 Phytoplankton Enumeration

Phytoplankton cells were enumerated at 100x magnification using the Utermöhl sedimentation technique (Utermöhl, 1958). Depending on cell densities, 3 to 7 mL aliquots were settled in a settling chamber for 36 hours prior to counting. Duplicate counts were made to counter variance from colonial cyanobacteria which constituted a high proportion of the phytoplankton community. Cell counts for filamentous species (*Anabaena planktonica*, *Anabaena circinalis*, *Aulacoseira granulata* var., and *Fragilaria crotonensis*) were derived from the average number of cells per trichome and counts of the number of trichomes present in samples (Ryan et al., 2003). Densities of colonial species (*Chlorokybus* sp., *Microcystis aeruginosa*, *Sphaerocystis* sp.) were calculated similarly, using the average number of cells per colony in each sample. Species were identified according to the identification guides of Baker and Fabbro (1999) and John et al. (2002). Species densities were converted to algal biomass (µm^3 mL^{-1}) using the average geometric shape of the algal units (Hillebrand et al., 1999). Net rates of phytoplankton growth over the incubation period, based on species biomass, were calculated using the equation (Reynolds, 1997):

$$r_n = \frac{\ln(N_t / N_0)}{t} \qquad (3.2)$$

where r_n is the growth rate (day^{-1}) and N_t and N_0 are cell densities at times t and 0 respectively.

3.2.3 Modelling

A phytoplankton growth model was applied to provide insights into the interacting effects of limitation by P, N and light (Robson and Hamilton, 2003):

$$\mu_{net} = \mu_{\max} f(T)\min[f(I), f(N), f(P)] - Rv^{(T-20)} \qquad (3.3)$$

where μ_{max} is the growth rate at 20 °C in the absence of any significant light or nutrient limitation, $f(T)$ is a temperature function, $f(I)$, $f(N)$ and $f(P)$ represent limitation by light, nitrogen and phosphorus, respectively, R is a loss term for the combined effects of natural mortality, respiration, zooplankton grazing and other loss processes at 20 °C and v is a constant governing the temperature response of these processes. In this application, it was assumed that only one parameter (light, P or N) would limit phytoplankton growth at any given time (Elliot et al., 2001; Robson and Hamilton, 2004). While the interacting effects of light and nutrients on growth are suggested to occur (e.g. Schallenberg and Burns, 2004), a minimum expression has been suggested to provide a more realistic model representation of growth limitation (Rhee and Gotham, 1981) and there are uncertainties in the water in which the interacting effects of light and nutrients might be combined in a numerical expression. Carbon, micronutrients and trace elements were also assumed not to be limiting (cf. White et al., 1978). Light limitation in the absence of photo inhibition was estimated using the model of Webb et al. (1974):

$$f(I) = 1 - \exp\left(\frac{-I}{I_{Ki}}\right) \qquad (3.4)$$

where I is the incoming irradiance, derived from Rotorua airport climate station, and I_{Ki} is the irradiance parameter for non-photoinhibited phytoplankton growth. A Michaelis-Menten equation was used to represent $f(N)$ and $f(P)$ terms as a function of water column nutrient concentrations:

$$f(N) = \frac{NO_3 + NH_4}{K_{Ni} + (NO_3 + NH_4)} \quad (3.5)$$

$$f(P) = \frac{PO_4}{K_{Pi} + (PO_4)} \quad (3.6)$$

where K_{Ni} and K_{Pi} are half saturation constants for nitrogen and phosphorus limitation, respectively. Values of K_{Pi} and K_{Ni} for the major cyanobacterial species in Lake Rotorua (*A. planktonica* and *M. aeruginosa*) were derived from Holm and Armstrong (1981) and Robson and Hamilton (2004). A value of 500 µmol quanta m^{-2} s^{-1} for I_{ki} was derived from Wallace and Hamilton (1999) for *Microcystis aeruginosa*, which was the species with the highest mean biomass over all three incubations.

A sensitivity analysis was carried out for each of these parameters by adjusting I_{ki} between 120 and 500 µmol quanta m^{-2} s^{-1} and K_{Ni} and K_{Pi} in the range 0.03 to 0.045 mg L^{-1} and 0.006 to 0.03 mg L^{-1}, respectively. The loss rate (R) was set to 0.1 day^{-1} (Robson and Hamilton, 2003). The model was run on an hourly time-step for four days, commencing at the same time as the *in situ* incubation experiments. Hourly values of incoming irradiance were derived from Rotorua Airport climate station.

3.3 Results

3.3.1 Physico-chemical results

Initial concentrations of dissolved nutrients (NH_4, NO_3 and SRP) and chl-*a* in the surface-mixed layer (0 to 8 m), and mean K_d, I'_0 and euphotic depth (z_d) for each incubation period are given in Table 3.1. Lake Rotorua was thermally stratified during incubations 1 and 2, when differences in temperature between surface and bottom waters exceeded 4 °C on some days, and fully mixed during incubation 3 (Fig. 3.2a). Longer stratification events were accompanied by low dissolved oxygen (Fig. 3.2a) and increases in NH_4 and SRP concentrations in bottom waters (Fig. 3.2b). Concentrations of NH_4 and SRP in surface waters were considerably higher at the start of incubation 3, when the water column was well mixed, than at the start of incubations 1 and 2. Initial mass ratios of TP:TN and dissolved inorganic nitrogen

Table 3.1: Initial conditions for each of the three incubations (periods 1-3). Nutrient concentrations are given for the surface-mixed layer (0-8 m) and for molar ratios of total nitrogen to total phosphorus (TN:TP) and dissolved inorganic nitrogen to soluble reactive phosphorus (DIN: SRP, where DIN = NO_3 + NH_4). Days represent incubation length.

Period	Start date	Days	NH_4	NO_3	SRP	TN:TP	DIN:SRP	Chl-*a*	K_d	z_d	$I'_{0.5}$	I'_S
			mg L^{-1}	mg L^{-1}	mg L^{-1}			ug L^{-1}	m^{-1}	m	μ mol quanta	m^2 s^{-1}
1	23-Jan 04	5.9	0.054	0.021	0.010	17.4	7.1	39.33	0.93	4.9	373.1	8.5
2	30-Jan 04	4.3	0.072	0.047	0.017	19.1	7.0	40.33	0.77	3.7	170.6	5.3
3	9-Feb 04	4	0.278	0.029	0.022	13.8	14.1	32.66	0.81	4.1	252.0	6.7

(DIN): dissolved inorganic phosphorus (DIP) ranged between 14 and 19, and 7 and 14, respectively, in the three incubations (Table 3.1). Initial concentrations of chl-*a* ranged from 33 to 40 μg L^{-1} for the three incubations, and average daily light irradiance was highest during incubation 1 and lowest during incubation 2.

3.3.2 Phytoplankton results

Thirteen phytoplankton species were recorded in Lake Rotorua during the course of the three incubations (Table 3.2). Cyanophyceae was the dominant taxonomic group, representing greater than 70 % of the total phytoplankton biomass in each of the three initial samples. *Anabaena planktonica* and *Microcystis aeruginosa* were the dominant cyanobacteria in all incubations, with *M. aeruginosa* dominant in incubations 1 and 3 (57 and 42 %, respectively) and *A. planktonica* dominant in incubation 2 (57 %). Biomass of *M. aeruginosa* and *A. planktonica* ranged from 313 to 1377 x 10^4 and 443 to 1220 x 10^4 μm^3 mL^{-1}, respectively. Chlorophyceae represented 22 % of the total average biomass and were dominated by *Chlorokybus* sp., which ranged in biomass from 281 to 533 x 10^4 μm^3 mL^{-1}. There was relatively high biomass of *Spaerocystis* sp. in incubation 1 (155 x 10^4 μm^3 mL^{-1}) compared with incubations 2 and 3 (51 and 11 x 10^4 μm^3 mL^{-1}, respectively). By comparison, Bacillariophyceae and other taxonomic groups constituted less than 1.5 % of the total biomass.

Chlorophyll *a* concentrations increased in each incubation, and N+P additions produced greatest growth response (Figs 3.3 and 3.4), although not all increases were statistically significant at $P < 0.05$ (Table 3.3). Chlorophyll *a* in N+P treatments increased by > 90 % in surface incubations and 43 % on average in 5 m incubations. Treatments of N and N+P produced chl-*a* concentrations that were significantly

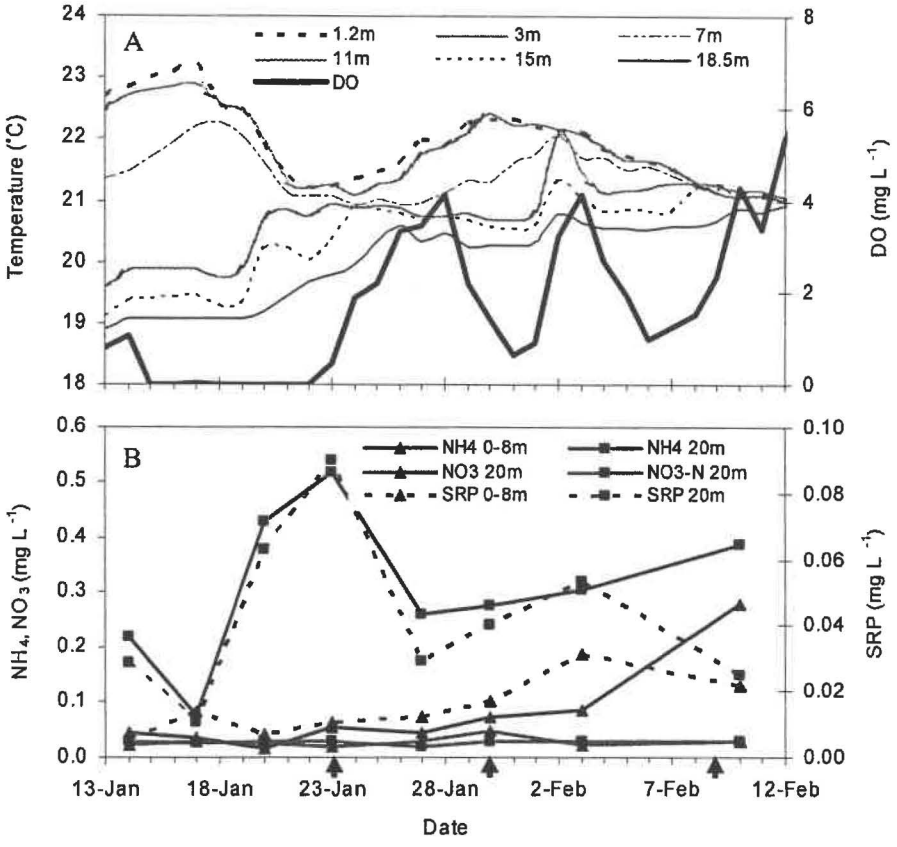

Figure 3.2: (A) Temperature and concentrations of bottom dissolved oxygen (DO), and (B) surface and bottom ammonium (NH_4), nitrate (NO_3) and soluble reactive phosphorus (SRP) concentrations, 13 Jan. to 12 Feb. 2005. The three incubation start dates are indicated by arrows in B.

different than those of the control at both depths for incubation 2, while for incubation 3, chl-*a* concentrations were significantly different in the N+P treatment at the surface and in the N treatment at 5 m.

Total phytoplankton biomass showed the greatest increase in all but one of the N+P incubations (Figs 3.3 and 3.4) although results were statistically significant only for surface incubations 2 and 3 (Table 3.3). Total biomass increased by at least 60 %, corresponding to increases of 1356 to 7904 x 10^4 μm^3 mL^{-1} for surface incubations and 2638 to 4764 x 10^4 μm^3 mL^{-1} for 5 m incubations. Total biomass decreased in the N+P treatment at 5 m in incubation 2. Additions of P alone yielded a greater response than N addition for biomass in all surface incubations and in two of three 5 m incubations; results of P addition were statistically significant in incubations 1 and 2 at 5 m (Table 3.3). For P addition to surface samples, biomass increased by 400, to

5131 x 10^4 μm^3 mL^{-1} (16-128 %), and for N addition from zero to 4590 x 10^4 μm^3 mL^{-1} (0-115 %). In the 5 m incubations, increases in biomass with P addition ranged from 1305 to 2659 x 10^4 μm^3 mL^{-1} (42-115 %) and with N addition from 1207 to 2596 x 10^4 μm^3 mL^{-1} (45- 83 %).

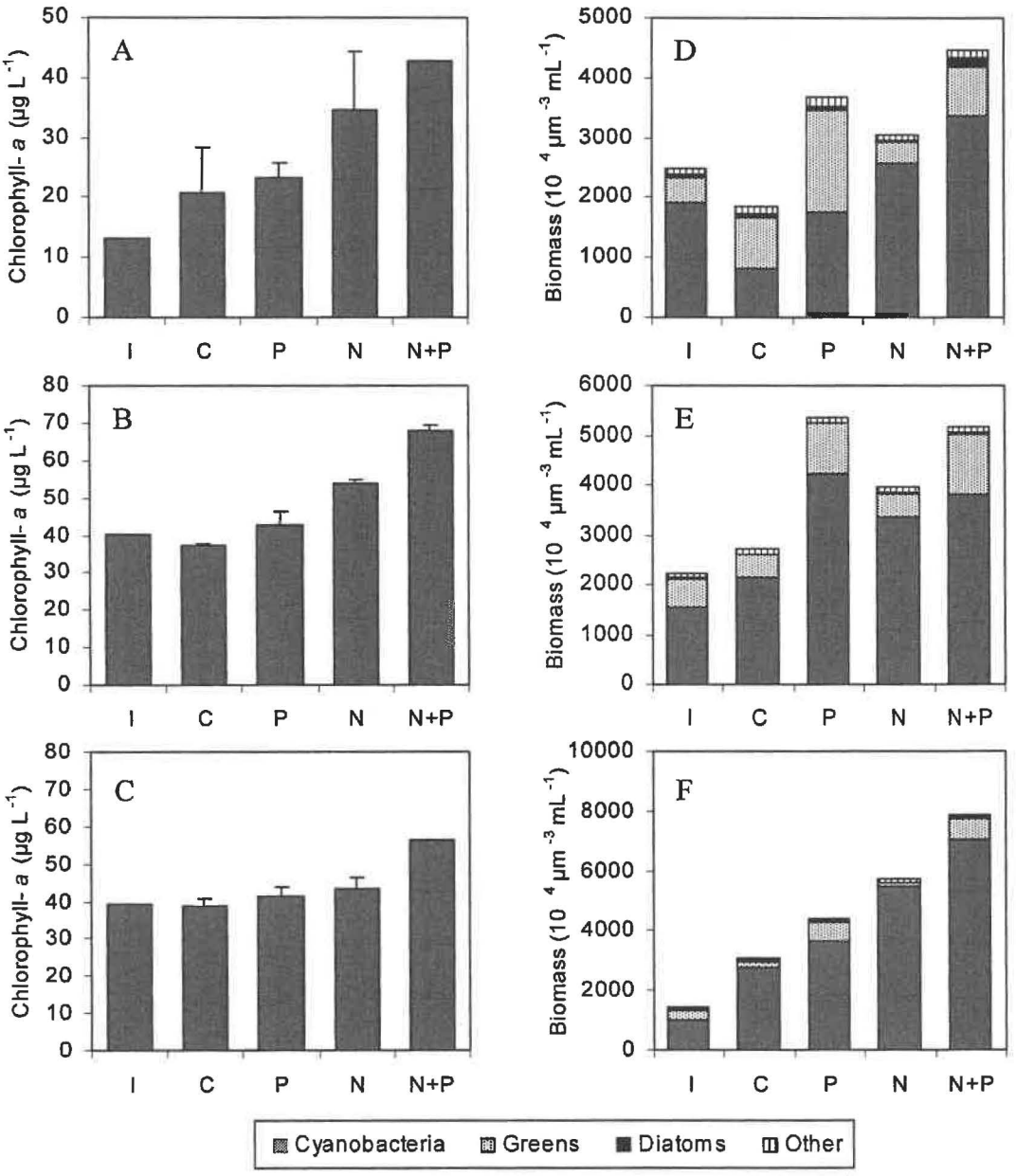

Figure 3.3: (A, B, C) Chlorophyll *a* concentration and (D, E, F) phytoplankton biomass by group, 0.5 m depth incubations for (A, D) 23 Jan., (B, E) 30 Jan. and (C, F) 9 Feb., 2004. I = initial concentration, C = control, P = phosphorus addition (0.1 mg L^{-1}), N = ammonium addition (1 mg L^{-1}), and N+P = phosphorus + ammonium addition. Error bars represent standard errors.

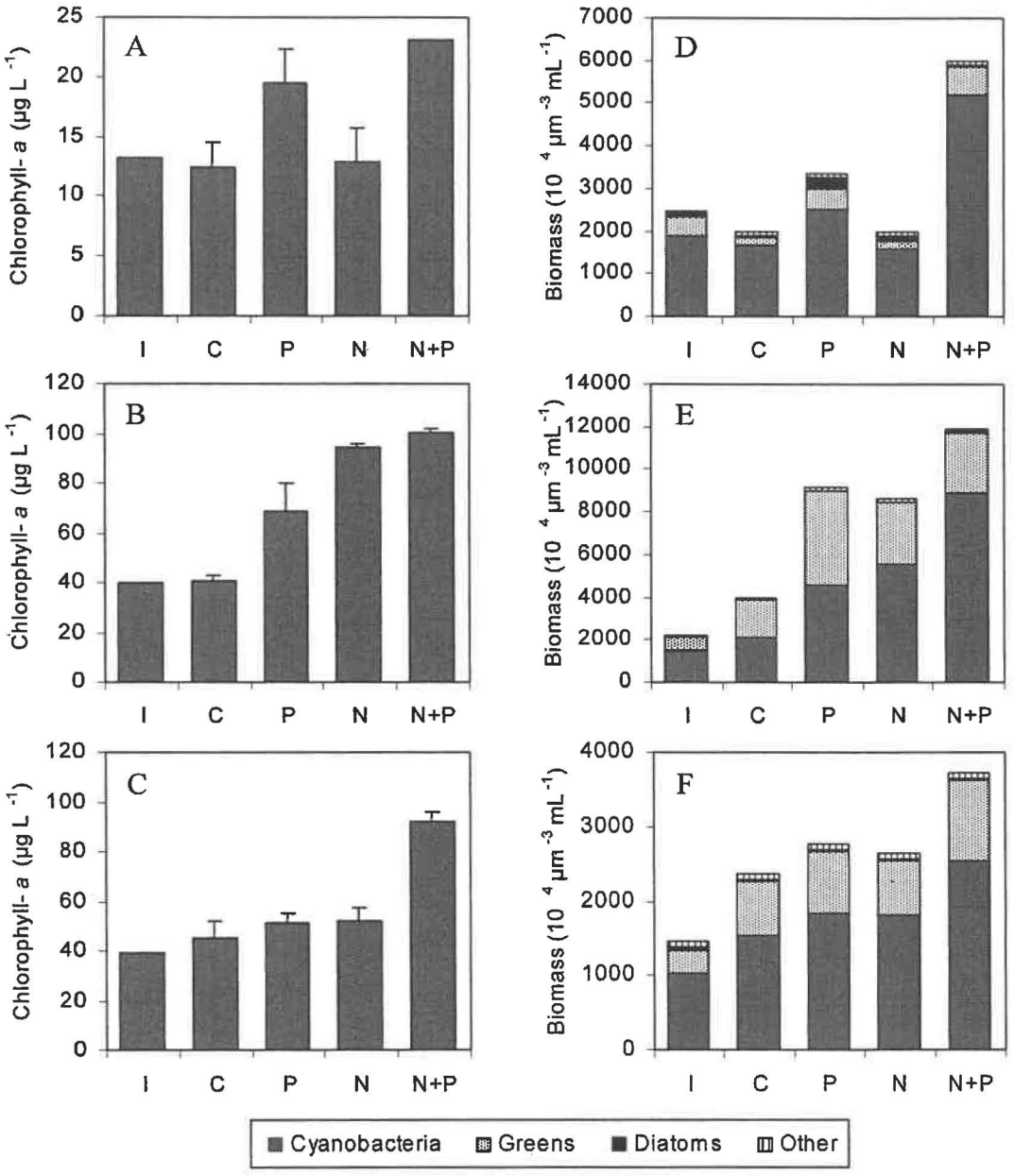

Figure 3.4: (A, B, C) Chlorophyll *a* concentration and (D, E, F) phytoplankton biomass by group, 5.0 m depth incubations for (A, D) 23 Jan., (B, E) 30 Jan. and (C, F) 9 Feb., 2004. I = initial concentration, C = control, P = phosphorus addition (0.1 mg L^{-1}), N = ammonium addition (1 mg L^{-1}), and N+P = phosphorus + ammonium addition. Error bars represent standard errors.

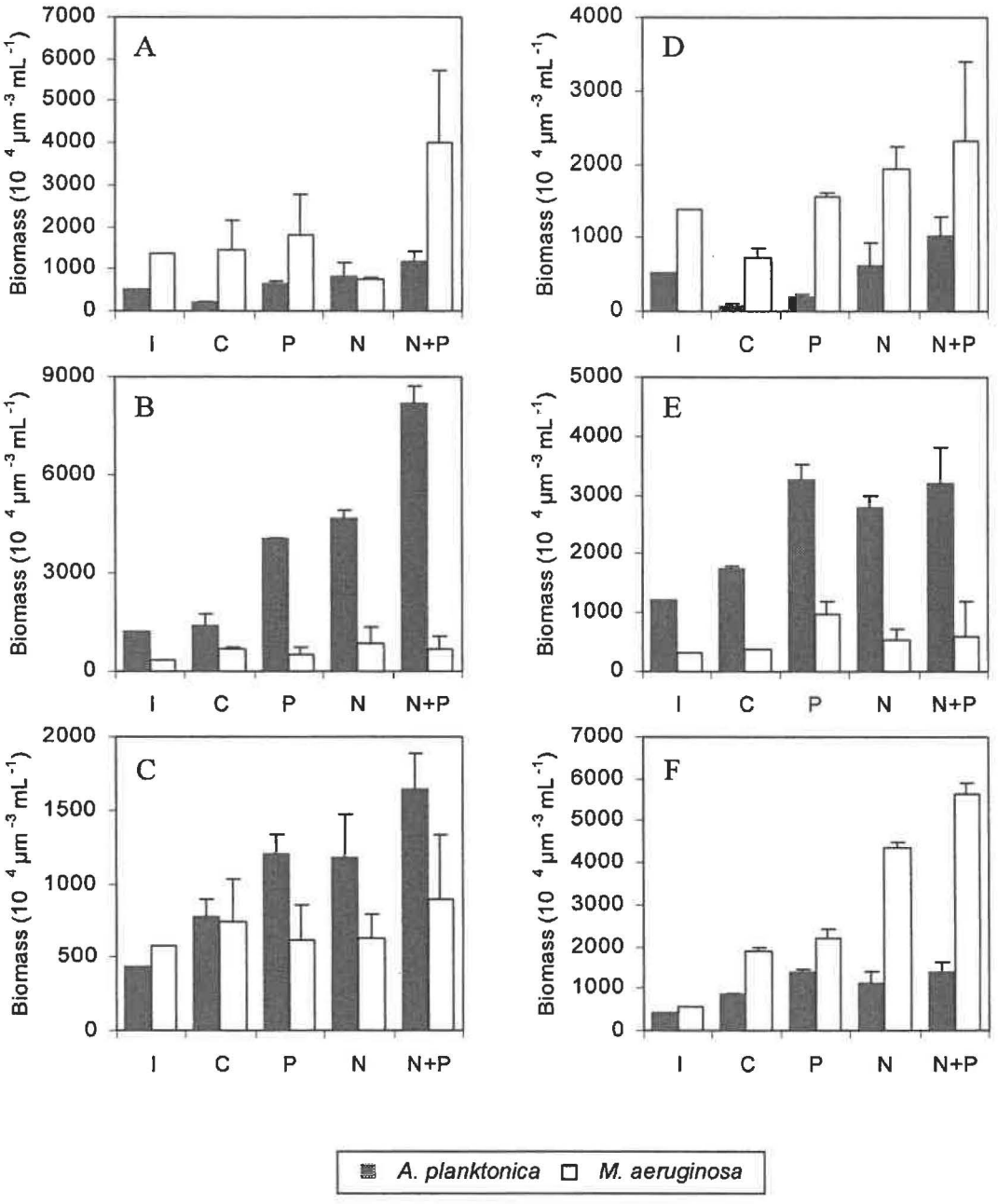

Figure 3.5: Biomass of *Anabaena planktonica* and *Microcystis aeruginosa* in (A, B, C) surface and (D, E, F) 5 m depth incubations, for (A, D) 23 Jan., (B, E) 30 Jan. and (C, F) 9 Feb., 2004. I = initial concentration, C = control, P = phosphorus addition (0.1 mg L^{-1}), N = ammonium addition (1 mg L^{-1}), and N+P = phosphorus + ammonium addition. Error bars represent standard errors.

Table 3.2: Phytoplankton biomass at the start of each incubation experiment (Jan. 24, Jan. 29 and Feb. 10, 2004), and mean community composition for the three incubations (1, 2 and 3). Samples were collected from the surface-mixed layer (0-8 m) at site 1.

Phyla	Species	1	2	3	Composition	Composition
		(10^4 μm^{-3} mL^{-1})			%	%
Cyanophyta	*Anabaena circinalis*	<1	<1	<1	0.00	75.47
	Anabaena planktonica	525	1220	443	37.09	
	Microcystis aeruginosa	1377	313	574	38.38	
	Planktothrix sp.	<1	<1	<1	0.00	
Chlorophyta	*Chlorokybus* sp.	281	533	313	19.09	22.89
	Eudorina sp.	<1	<1	<1	0.00	
	Spaerocystis sp.	155	51	11	3.68	
	Staurastrum sp.	<1	3	4	0.12	
Bacillariophyta	*Aulacoseira granulata* var.	36	<1	15	0.87	1.22
	Cocconeis placentula	<1	<1	<1	0.00	
	Fragilaria crotunensis	21	<1	<1	0.36	
Euglenophyta	*Trachelomonas volvocina*	<1	<1	<1	0.00	0.00
Phyrrophyta	*Peridinium small* (gymnoid)	12	13	<1	0.42	0.42

Table 3.3: One-way analysis of variance (ANOVA) of chlorophyll *a* concentration and biomass of dominant phytoplankton species and taxonomic groups for different treatments compared with control treatment. Cells denoted by P, N and N+P represent a significant difference ($P < 0.05$) between the control and phosphorus, nitrogen or nitrogen + phosphorus additions, respectively. Higher levels of significance are denoted by * for $P < 0.01$.

Incubation depth (m)		**0.5**			**5**	
Period	**1**	**2**	**3**	**1**	**2**	**3**
Chlorophyll-*a*	-	N*, N+P*	NP	-	N*, N+P*	N*
Species						
Anabaena. planktonica	N, N+P	P, N+P*	-	-	P	-
Microcystis aeruginosa	-	-	-	P	-	-
Chlorokybus sp.	P	-	-	-	P	-
Spaerocystis sp.	NP	-	-	P	-	-
Group						
Total cyanobacteria	-	P, N, N+P*	-	P	P, N+P	-
Total chlorophyceae	P	-	-	P	P	-
Total bacillariophyceae	P	-	-	-	-	-
Total algae	-	N+P	N+P	P*	P	-

Increases in biomass of cyanobacteria ranged from 1029 to 2529 x 10^4 μm^3 mL^{-1} (66-325 %) over the three incubation periods at two depths. Cyanobacteria were the dominant taxonomic group in all incubations and their biomass increased most with N+P addition, though results were statistically significant ($P < 0.05$) on only two occasions (Table 3.3). For single nutrient additions, increases in cyanobacteria biomass were statistically significant for P addition in incubations 1 and 2 at 5 m, and for N addition and P addition in surface incubation 2.

At a species level, *A. planktonica* biomass increased significantly ($P < 0.05$) in N and N+P additions in surface incubation 1, P and N+P in surface incubation 2, and P at 5 m in incubation 2 (Table 3.3). *M. aeruginosa* biomass response was greatest to N in the two 5 m incubations, although results were significant only in incubation 2. Decreases in *M. aeruginosa* biomass that occurred in some surface incubations were not significant (Fig. 3.5). Maximum growth rates for cyanobacteria species, based on maximum rates of biomass increment, were 0.42 day^{-1} for *A. planktonica* and 0.30 day^{-1} for *M. aeruginosa*.

Biomass of chlorophyceae increased more with P addition than N addition in all incubations, with the results significant at $P < 0.05$ for incubations 1 and 2 at 5 m, and incubation 2 at the surface. Increases in biomass ranged from 88 to 2596 x 10^4 μm^3 mL^{-1} (11-139 %), and the average increase in the P incubations was 794 x 10^4 μm^3 mL^{-1}. Maximum growth rates based on biomass were 0.31 day^{-1} for *Chlorokybus* sp. and 0.23 day^{-1} for *Sphaerocystis* sp.

3.3.3 Model results

Model simulations of the three growth limitation factors (light, P and N) suggest that light limited phytoplankton growth more frequently than P or N over the three incubations and at the two depths (Table 3.4, Fig. 3.6). In surface incubations, light limitation occurred more than 69 % of the time for simulations with typical literature values for I_{ki}, K_{Pi} and K_{Ni} (Table 3.4). Light limitation occurred for the greatest proportion of time in incubation 2 (98 %), coinciding with low irradiance. Phosphorus limitation occurred on average 13 % of the time and N limitation occurred only briefly in incubation 1 (8 %). P limitation was also greatest for incubation 1, when the lake was stratified and water column nutrient concentrations

were lower than for the first two incubations. For the 5 m incubations, light was always limiting, with no periods of P or N limitation (Fig. 3.6).

A sensitivity analysis of the model parameters showed the model to be most sensitive to I_{ki}. Similar responses in light, P and N limitation where observed between model run 2, when only I_{ki} was altered and model run 6, when all three parameters were altered (Table 3.4). Under all scenarios tested, light limitation occurred at least 48 % of the time in all incubations (Table 3.4). However, at low irradiance (incubation 2), P limitation increased by 38 % when I_{ki} was reduced from 500 to 120 (μmol quanta m^{-2} s^{-1}), and by 33 % when K_{Pi} was increased from 0.006 to 0.009 mg L^{-1}. The incidence of N limitation also increased 24 % in incubation 2 when K_{Ni} was increased from 0.03 to 0.045 mg L^{-1}. Light limitation was simulated to occur continuously in all incubations at 5 m.

Table 3.4: Parameter values and model results for phytoplankton limitation factors in the control bottles during each surface incubation (Jan. 24 and 29, and Feb.10, 2004), where % $f(I)$ represents percent of light limitation over the four-day incubation, % $f(P)$ is percent phosphorus limitation and % $f(N)$ is percent nitrogen limitation. Parameters were derived from Holm and Armstrong (1981, I_{Pi}), Wallace and Hamilton (1999, I_{ki}) and Robson and Hamilton (2004, I_{Ni}).

Model Run		**1**	**2**	**3**	**4**	**5**	**6**
Parameters	I_{ki} ($\mu Em^{-2}s^{-1}$)	530	120	530	530	530	120
	K_{Pi} ($mg\ L^{-1}$)	0.006	0.006	0.009	0.006	0.009	0.009
	K_{Ni} ($mg\ L^{-1}$)	0.03	0.03	0.03	0.045	0.045	0.045
Results							
Incubation 1	**% f (i)**	69	63	95	95	94	61
	% f (P)	23	18	5	0	6	18
	% f (N)	8	20	0	5	0	22
Incubation 2	**% f (i)**	98	49	65	69	65	48
	% f (P)	2	40	35	7	27	41
	% f (N)	0	10	0	24	8	10
Incubation 3	**% f (i)**	86	64	81	86	81	59
	% f (P)	14	36	19	14	19	41
	% f (N)	0	0	0	0	0	0
Average of all incubations	**% f (i)**	84	59	80	83	80	56
	% f (P)	13	31	20	7	17	33
	% f (N)	13	31	20	7	17	33

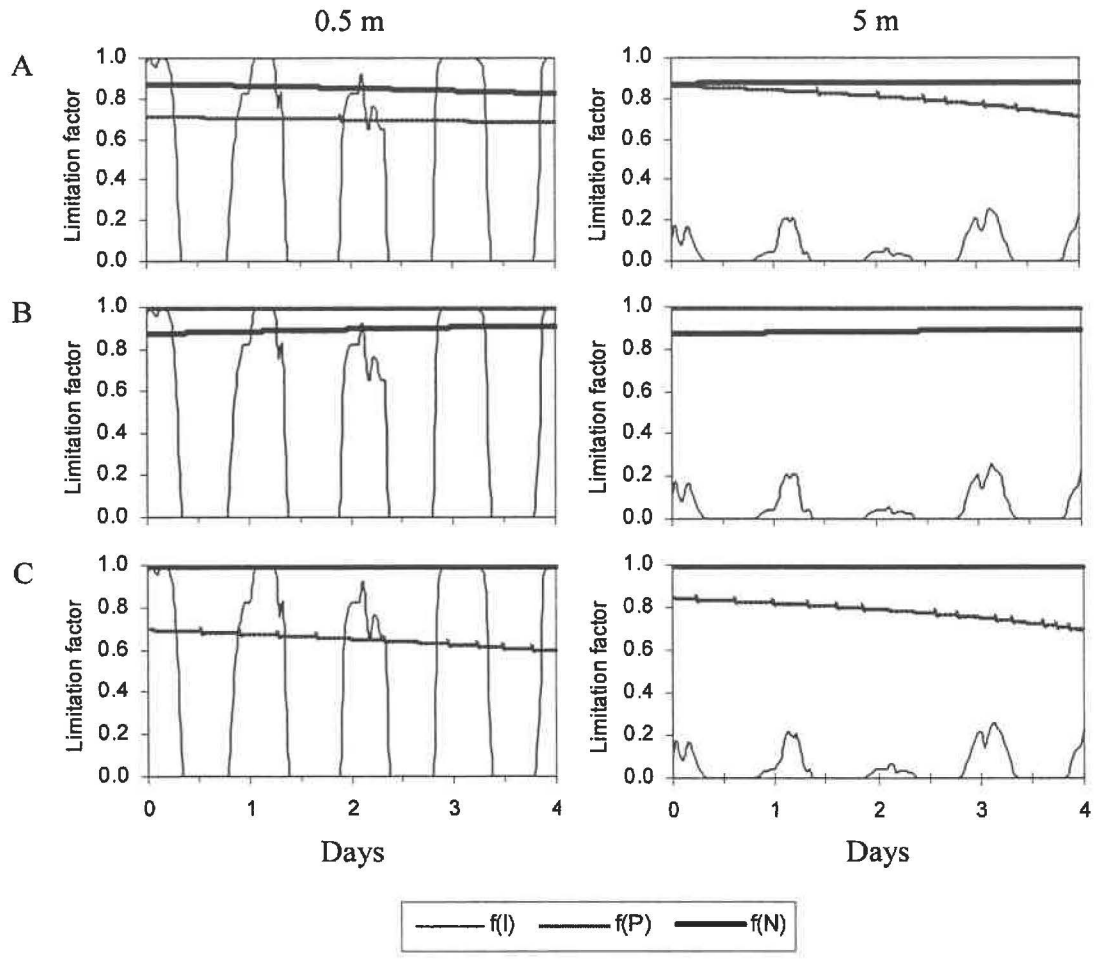

Figure 3.6: Simulated phytoplankton limitation factors in (A) control, (B) +P, and (C) +N bottles at the surface (left) and at 5 m depth (right) for incubation 3. $f(I)$, $f(P)$ and $f(N)$ are limitation factors for light, nitrogen and phosphorus, respectively.

3.4 Discussion

Increases in chl-*a* concentration and total phytoplankton biomass occurred in all incubations with nutrient additions, suggesting that the Lake Rotorua algal community is nutrient limited. These increases were generally greatest in the N+P incubations, a result similar to that observed in many other nutrient bioassay experiments conducted across a wide variety of lake types, as reviewed by Elser et al. (1990). Phytoplankton biomass responses to nutrient additions were greatest for P addition, suggesting that this nutrient was most likely to limit growth. There were, however, several results that were not statistically significant, as well as differences in response between chl-*a* and phytoplankton biomass, and also within the phytoplankton community itself.

In Lake Rotorua, concentrations of bioavailable nutrients in the water column may vary due to the polymictic nature of the lake. Stratification is accompanied by deoxygenation and sediment nutrient release, and high concentrations of nutrients are mixed into surface waters with the breakdown of stratification. Total phytoplankton biomass, as well as cyanophyceae and chlorophyceae biomass, showed a significant response to P in incubations 1 and 2 at 5 m depth when the lake was stratified, but not in incubation 3 when the lake was well mixed and there were higher initial water column nutrient concentrations. This result suggests high concentrations of P resulting from release from lake sediments during stratification, with subsequent mixing, prevented the occurrence of nutrient limitation in incubation 3, and that nutrients derived from remobilisation from bottom sediments are important for sustaining high phytoplankton biomass in this lake.

Increases in chl-*a* concentrations were generally greatest for N addition, but this was not reflected in total phytoplankton biomass, which responded most to P addition. In previous nutrient limitation studies in Lake Rotorua, White and Payne (1978) and White et al. (1986) found that chl-*a* showed a consistent growth response to N in 4- to 5-day bioassay experiments, with physiological experiments also supporting N limitation (Vincent, 1984). As the phytoplankton community structure was not examined and incubations were conducted in the laboratory, it is difficult to directly compare these results with those obtained in the current study, to ascertain whether there has been a significant change in the limiting nutrient.

Phytoplankton increase cellular chl-*a* content in low-light and high-N environments, though this response is also quite species-specific (Venrick, 1988; Shortreed and Stockner, 1990; Kirk, 1994), most likely in association with N being a functional constituent of the chl-*a* molecule, and not P (Meeks, 1974). White and Payne (1978) suggested that N additions may lead to overestimates of chl-*a* production, but that the consistent growth response to N additions observed in their fertilisation experiments conducted between 1975 and 1976, along with only minor growth response to P, was indicative of N limitation in Lake Rotorua.

While the phytoplankton community as a whole appeared to respond mostly to P addition, some species showed a greater response to N on occasions. Cyanobacterial

biomass responded most to N addition in two of the three incubations conducted at depth 5 m, when *M. aeruginosa* was the dominant phytoplankton. This species is highly competitive in high-N, low-light environments. *Anabaena planktonica* also showed a greater growth response to N than P on three occasions, with no clear trend between the two incubation depths. In all incubations, chlorophyceae response was greatest to P additions, suggesting that P was the dominant nutrient limiting these species in Lake Rotorua.

Phytoplankton communities may be limited by more than one nutrient as different species have different optimum nutrient ratios for growth (Hecky and Kilham, 1988). As nutrient bioassay experiments routinely use only chl-*a* to quantify nutrient limitation, it is likely that some of the variability in response is contributed by presence of different dominant populations of phytoplankton amongst the community assemblage. Genera-specific responses have been documented in a river system by Mitrovic et al. (2001) and the marine environment by Lagus et al. (2004), but our study is the first to demonstrate species specific responses to nutrient additions in a freshwater lake.

There are many other variables that may have played a role in our results, but were not examined in this study. For example, luxury uptake of P, or possibly N, and variations in internal nutrient stores at the outset of the incubations, may confound expected linear responses of phytoplankton to additions of a limiting nutrient. The results of White et al. (1985) suggest cellular storage capacities of up to 5 times the subsistence level for P and 0.5 times for N, based on bioassay experiments conducted in 12 North Island volcanic lakes, including Lake Rotorua. Certain heterocystous cyanobacteria, including *A. planktonica*, also have the ability to fix atmospheric nitrogen, particularly during periods of N limitation. However, in this study very few cyanobacterial filaments (< 1 %) were observed to be heterocystous.

Phytoplankton may also be limited by carbon. Lake Rotorua has low concentrations of dissolved inorganic carbon (2.5 g C m^{-3}, Timperley, 1987), close to levels that have been found in other studies to limit the rate of photosynthesis (Hein, 1997). It is possible in the 4-day incubations in Lake Rotorua, that carbon limitation may have been induced due to moderately high phytoplankton biomass and isolation from

external C sources. Analysis of inorganic carbon concentrations should therefore be conducted routinely in bioassay experiments of more than 1 to 2 days.

Model simulation results of the incubations suggested that light limited phytoplankton growth more frequently than P or N. The surface-mixed layer in Lake Rotorua is typically around 8 to 10 m depth, and the incubations conducted at 5 m can therefore be considered to represent mean light levels available to phytoplankton populations in the lake. The simulations also showed that light always limited growth at this depth, even when model parameters were varied as part of a sensitivity analysis. Havens (1998) suggests that underwater irradiance controls cyanobacteria species composition and biomass in shallow lakes, and phytoplankton have also been observed to be co-limited by both light and nutrients (e.g., Knowlton and Jones, 1996; Ferber et al., 2004; Schallenberg and Burns, 2004), but there is still more work required to elucidate the nature of interactions amongst light and nutrient interaction.

Nutrient concentrations in Lake Rotorua often approach levels that could saturate growth (White et al., 1985). Thus, nutrient loading to this lake must be reduced substantially in order to exert major controls on phytoplankton biomass. Levine and Schindler (1999) suggest reducing P is the most cost-effective method for managing cyanobacteria as both non-heterocystous and heterocystous species favour high P. However, in Lake Rotorua, although P appeared to be more important in limiting the phytoplankton, the possibility of N limitation should not be neglected and only simultaneous reduction of both nutrients is likely to reduce biomass, including cyanobacterial populations.

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Chapter 4: Phosphorus and nitrogen sedimentation in Lake Rotorua[1]

Abstract

Sedimentation rates of total particulate matter (TPM), total phosphorus (TP), total nitrogen (TN) and chlorophyll *a* (chl-*a*) were determined seasonally at three sites in polymictic, eutrophic Lake Rotorua. Deployment of sediment traps at different depths at each site showed an increase in sedimentation rates of particulate inorganic material, and a decrease in TP:TN molar ratios, with trap depth, indicating that sediment resuspension is an important process in this lake. Resuspension was estimated to contribute up to 71 % of TPM sedimentation at the shallowest site. Net sedimentation rates across all sites, excluding resuspension fluxes, were 4.5 g m^{-2} d^{-1} for TPM, and 19.8, 103.7 and 42.1 mg m^{-2} d^{-1} for TP, TN and chl-*a*, respectively. Sedimentation rates of all variables were highest in summer and at the deepest sampling site. Mean net sedimentation rates of N and P were between four (N) and nine (P) times greater than estimates of net retention based on a nutrient mass balance, demonstrating that internal nutrient recycling is an important process in Lake Rotorua. This has important implications for the management of this lake, as improvements in lake water quality will be delayed following reductions in external nutrient loading.

4.1 Introduction

Sedimentation is an important component of the internal nutrient cycle in lakes as it regulates loss of organic and inorganic particulate material from the water column and controls supply of nutrients to the bottom sediments (Gálvez and Niell, 1992). High supply rates of organic matter to the bottom sediments may be important in sustaining high rates of sediment nutrient release, particularly in eutrophic lakes (Marsden, 1989; Kleeberg and Kozerski, 1997; Søndergaard et al., 2003).

[1] To be submitted to *New Zealand Journal of Marine and Freshwater Research* as: D.F. Burger, D.P. Hamilton, M. M. Gibbs and C. P. Pilditch: Phosphorus and nitrogen sedimentation in Lake Rotorua, New Zealand.

Sedimentation also affects phytoplankton productivity, either directly through its influence on the longevity of negatively buoyant phytoplankton cells in the water column, or indirectly through its influence on bioavailable nutrients regenerated from particulate organic and inorganic material (Gálvez and Niell, 1992; Nõges et al., 2000). Quantifying sedimentation rates is therefore essential to determine fate and transport of nutrients, as well as to quantify the processes influencing phytoplankton dynamics.

Sedimentation rates in lakes vary seasonally due to changes in phytoplankton community structure and biomass, and physical conditions such as wind-induced turbulence and stratification (Guy et al., 1994; Koski-Vähälä et al., 2000; García-Ruiz et al., 2001). Sedimenting material includes not only 'new' organic material derived from primary production, but also resuspended bottom material brought into the pelagic zone by wave and current induced turbulence (Kozerski, 1994; Bloesch, 1995). Resuspension may be particularly important in large shallow lakes (Bloesch, 1995) and in some cases the proportion of sedimenting material due to resuspension exceeds 90 % of the total flux (Weyhenmeyer et al., 1995).

Cylindrical sediment traps (e.g., Chalar and Tundisi, 2001; Kleeberg, 2002) provide the most direct means of quantifying gross deposition rates and their spatial and temporal variations (see reviews by Bloesch and Burns, 1980; Gardner, 1980; Blomqvist and Håkanson, 1981 and Butman, 1986). Short-term (i.e., hours to days) deployments provide a direct measure of sedimentation, for which corrections can be applied for the contribution of resuspended material (Gálvez and Niell, 1992; Bloesch, 1994).

In eutrophic Lake Rotorua, we hypothesise that high rates of release of dissolved nutrients from the bottom sediments (Burger et al., 2005) are sustained primarily by correspondingly high rates of sedimentation. In order to better understand internal nutrient recycling processes in this lake, the primary objective of this study was to examine spatial variations in sedimentation rates associated with a shallow littoral site versus deeper pelagic zone sites. A secondary objective was to provide indirect measures of sediment resuspension in Lake Rotorua based on vertical differentiation of sediment deposition rates through the water column.

4.1.1 Study site

Lake Rotorua is a large (79.8 km^2), shallow (mean depth 10.8 m) lake of volcanic origin in central North Island, New Zealand (Fig. 4.1). The lake is polymictic and stratifies intermittently over summer. The duration of each stratification event ranges from days to weeks (Burger et al., 2005). Lake Rotorua is eutrophic (Rutherford et al., 1996) and annual mean concentrations of total phosphorus (TP) and nitrogen (TN) are 0.055 mg L^{-1} and 0.814 mg L^{-1}, respectively. The lake has a catchment area of 425 km^2 which is dominated by agriculture (48 %) and plantation forestry (23 %). Inflows to the lake can be separated into nine major streams (mean flow 0.2-2.8 m^3 s^{-1}) and 17 minor streams, urban drains and geothermal springs (mean flow < 0.06 m^3 s^{-1}) . The Ohau Channel is the only surface outflow and the lake has a water residence of c. 530 days.

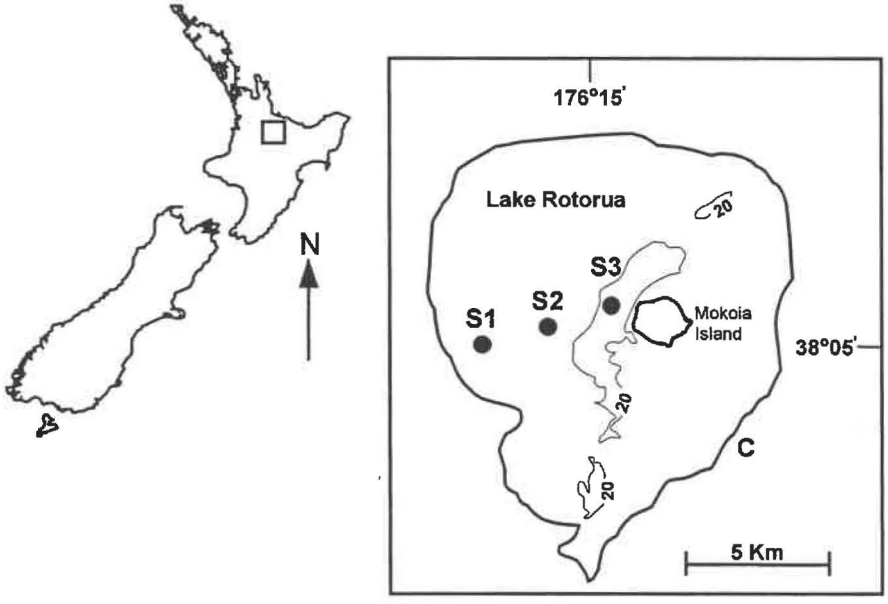

Figure 4.1: Map of Lake Rotorua showing sites 1 (S1, depth 7 m), 2 (S2, depth 14 m) and 3 (S3, depth 20 m). The 20-m depth contour and Rotorua Airport climate station (C) are also shown.

4.2 Methods

4.2.1 Sedimentation Rates

Sedimentation rates were measured with cylindrical sediment traps (PVC, 0.065 m diameter, 0.65 m height) that conformed to the aspect ratio calculated by Bloesch and Burns (1980) to prevent resuspension of trapped material. Traps were deployed at

three sites (Fig. 4.1) on four sampling occasions (February, August and December 2003 and January 2004; Table 4.1). Sites were chosen to reflect the natural variability in mixing regime observed in the lake, from permanently well-mixed conditions in the littoral regions (site 1, water column depth, z = 7 m), to periodically stratified conditions in the deeper pelagic zone (site 2: z = 14 m, site 3: z = 20 m). At site 3, traps were placed at 5, 12, 15 and 18 m depth and at site 2, at 5, 9 and 12 m depth. At site 1 traps were deployed only at one depth in the water column (5 m). At each trapping depth, four traps were supported by a wooden frame and attached to a central rope suspended vertically in the water column between a bottom anchor and a sub-surface buoy (z = 1.2 m). Replicate traps were separated by a distance of at least three times the trap diameter to minimise inter-trap hydrodynamic bias (Nodder and Alexander, 1999).

Seventy mL of 20 ppt NaCl solution were used in the base of each trap to minimise microbial decay and increase trapping efficiency (Gardner, 1980) and the remaining volume of each trap was filled with filtered water. Traps were deployed for a period of 4 to 6 days (Table 4.1), dependent on weather conditions. Trap deployment and retrieval were carried out with assistance from SCUBA divers. After the deployment period, plastic lids were clipped onto each trap to ensure trap contents were not lost during retrieval. Once retrieved, traps were settled for 30 minutes before supernatant water was siphoned off and the remaining 200-300 mL placed on ice and returned to the laboratory.

Samples were homogenised then sub sampled for analyses of TP and TN, chl-*a* and TPM. Unfiltered samples were frozen prior to analyses for concentrations of TP and TN in duplicate using a modified peroxodisulphate digestion for both nutrients (Ebina et al., 1983). Analyses were then conducted as for soluble reactive phosphorus (SRP) and nitrate (NO_3) on a Lachat Instruments flow injection analyser (FIA, Zellweger Analytics, 2000). Additional samples were filtered (Whatman GF/C, size 25 mm) and frozen for subsequent analysis of chl-*a* in duplicate (Turner Designs fluorometer), using acetone extraction and the spectro-fluorometric method of Arar and Collins (1992). Dry weight of suspended solids (SS) and particulate inorganic matter (PIM) were determined from duplicate samples filtered onto pre-combusted (550 °C) and pre-weighed filters (Whatman GF/C, size 47 mm). Filters were dried at 105 °C

overnight for determination of TPM, then combusted at 550 °C for 4 hours to determine particulate inorganic matter (PIM). Particulate organic matter (POM) was determined as the difference between TPM and PIM. All analyses were carried out on two (TP and TN) or three (TPM, POM, chl-*a*) of the traps from each trapping depth for replication

Duplicate samples for analyses of particulate organic carbon (POC) and particulate organic nitrogen (PON) were collected on two deployment dates (10 Feb. 2003 and 27 Jan. 2004) from two traps at each depth and site. Samples were filtered onto pre-combusted filters (Whatman GF/C, size 25 mm) before acidification to remove inorganic material (0.1 N H_2SO_4) and analysis using a CHN Elemental Analyser (Perkin-Elmer Model 240-C).

Water samples were also collected from each trapping depth at all three sites on the first and final day of deployments, using a Schindler-Patalas trap. These samples were analysed for TPM, POM, TP, TN, and chl-*a* using techniques identical to those used for trap samples. Conductivity-temperature-depth (CTD) profiles (Seabird Electronics), with additional CTD-mounted sensors for chl-*a* fluorescence (Chelsea Instruments Ltd) and dissolved oxygen (DO) concentrations (Seabird Electronics), were also taken at this time.

4.2.2 Calculations of sedimentation rate

Gross sedimentation rates to the sediments, as determined from trap deployments 2 m above the bottom at each site, were corrected for resuspension to determine net sedimentation rates. At sites with multiple trap depths (sites 2 and 3), the fraction, f_r, of TPM in the trap due to resuspension is given as (Kozerski, 1994):

$$f_r = \frac{r_B - r_U}{r_B} \qquad (4.1)$$

where r_B and r_U (g m^{-2} d^{-1}) are the net trapping rates in the bottom sediment trap and in a trap above the bottom trap, respectively. At site 1, where sediment traps were deployed at only one depth, f_r was calculated as (Gasith, 1976):

$$f_r = (f_{trap} - f_{WC})/(f_{sed} - f_{WC}) \quad (4.2)$$

where f_{trap} is the fraction of organic material in the trapped material, f_{WC} is the fraction of organic material in particulate matter from water at a depth immediately above the trap and f_{sed} the fraction of organic material in surficial bottom sediments (depth 0-5 mm) below the trap. Duplicate cores of the bottom sediments below site 1 were taken by SCUBA divers during each of the four trap deployments. The surficial sediments from these cores were treated identically to those of filters used for POM determination, with the mean of dried sediment lost during combustion used to determine f_{sed}. Gross sedimentation rates of chl-*a*, TN, TP, POC and PON were corrected for resuspension based on f_r estimates calculated from TPM.

4.2.3 Data Analysis

Differences in TPM, chl-*a*, TN and TP sedimentation rates among sites and among periods were examined using one-way analysis of variance (ANOVA) with *post-hoc* analysis using the Tukey HSD test with a confidence interval of 95 %. Prior to ANOVA analysis, data were examined for normality and homogeneity of variance by visual inspection of residuals and no transformations were necessary.

4.3 Results

4.3.1 Water column variables

The water column was thermally stratified at sites 2 and 3 in February 2003 and January 2004 (summer), with a mean thermocline depth, based on vertical density (ρ) gradient with depth z ($\partial\rho/\partial z$ = maximum), between 7 and 8 m (Fig. 4.2). The mean difference between surface and bottom water temperatures for these periods was 2 °C, and stratification was accompanied by reduced DO in the hypolimnion (Fig. 4.2). Site 1 remained well-mixed, however, with relatively constant DO through the depth profile. In August (winter) and December (early summer) 2003, the water column was isothermal at all sites and DO was nearly homogeneous vertically. Profiles of chl-*a* fluorescence indicated higher levels of phytoplankton biomass in summer (Feb. 2003 and Jan. 2004) than in winter (Aug. 2003; Fig. 4.2). There was high variability in fluorescence among sites and with depth at each site. For example, fluorescence

Table 4.1: Mean hourly wind speed at 10 m elevation (U_{10}) at Rotorua Airport climate station during each deployment, and spatially averaged (sites 1-3) total particulate material (TPM), chlorophyll *a* (chl-*a*), total nitrogen (TN) and total phosphorus (TP) concentration in the surface-mixed layer (0-8 m) (± SD).

Date	U_{10}	TPM	Chl-*a*	TN	TP
	m s^{-1}	mg L^{-1}	ug L^{-1}	mg L^{-1}	mg L^{-1}
10 -14 Feb. 2003	2.49±0.41	7.1±0.8	20.4±5.4	0.641±0.025	0.030±0.001
13 -18 Aug. 2003	2.99±1.07	3.4±0.3	9.8±7.6	0.427±0.040	0.085±0.013
1 - 5 Dec. 2003	2.82±0.56	5.8±0.8	21.0±2.6	0.900±0.341	0.061±0.051
27 - 30 Jan. 2004	3.13±0.38	10.7±9.6	60.4±22.9	1.325±0.098	0.049±0.015

averaged over the surface-mixed layer (0-8 m) and over the two summer samplings was approximately 30 % higher at site 2 than at sites 1 and 3.

Spatially averaged chl-*a* concentrations in the surface-mixed layer (0-8 m) over the three sites ranged from 9.7 μg L^{-1} in August 2003 to 60.4 μg L^{-1} in January 2004 (Table 4.1), with high variability between sites. Concentrations of TPM ranged from 3 mg L^{-1} (Aug. 2003) to 11 mg L^{-1} (Jan. 2004) while TN and TP concentrations ranged from 0.427 to 1.325 mg L^{-1} and 0.030 to 0.085 mg L^{-1}, respectively (Table 4.1).

Mean hourly wind speed, calculated over the full duration of deployment, varied little between the seasonal deployments, ranging from 2.6 m s^{-1} (Feb. 2004) to 3.2 m s^{-1} (Jan. 2004, Table 4.1). Hourly wind speed measurements were quite variable within individual seasonal deployments (Fig. 4.3) and there was a strong daily cycle in the wind speed, with strongest daily winds commonly mid-afternoon of each day for all periods (Fig. 4.3).

4.3.2 Sedimentation rates

Gross trapping rates of TPM generally increased with depth (Fig. 4.4). At site 3, traps at 18 m depth collected between 27 and 87 % more TPM than those at 15 m while at site 2, traps at 12 m collected up to 21 % more TPM than those at 9 m, except during January 2004. Mean gross trapping rates of TPM at site 1 were 40 % higher than those at the same depth at site 2, and 58 % higher than at the same depth at site 3.

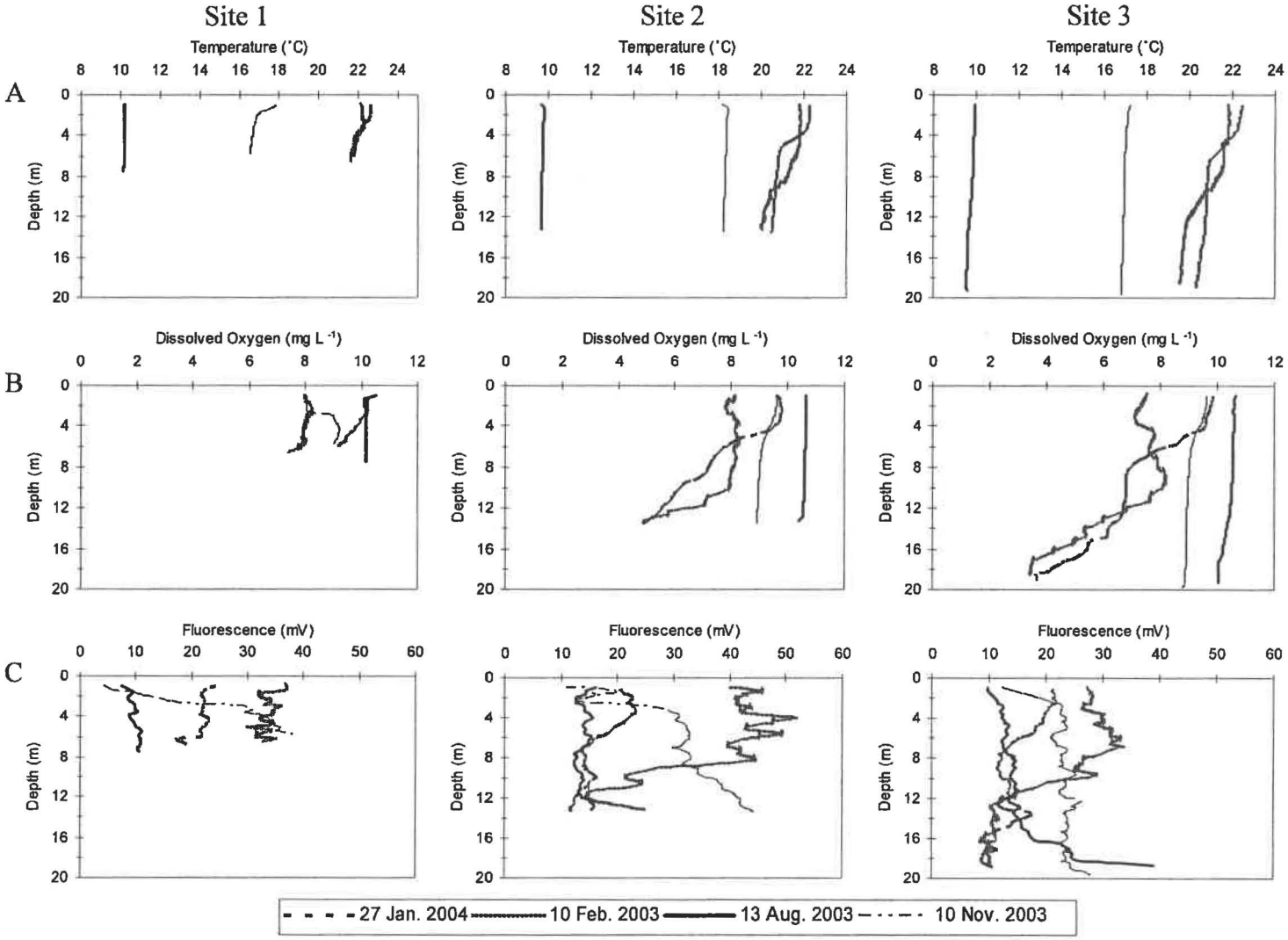

Figure 4.2: Water column profiles of (A) temperature, (B) dissolved oxygen concentration and (C) chlorophyll fluorescence at sites 1, 2 and 3 on 10 Feb., 13 Aug. and 1 Dec. 2003, and 27 Jan. 2004. Note: fluorescence readings may have been affected by quenching at water depths < 2 m.

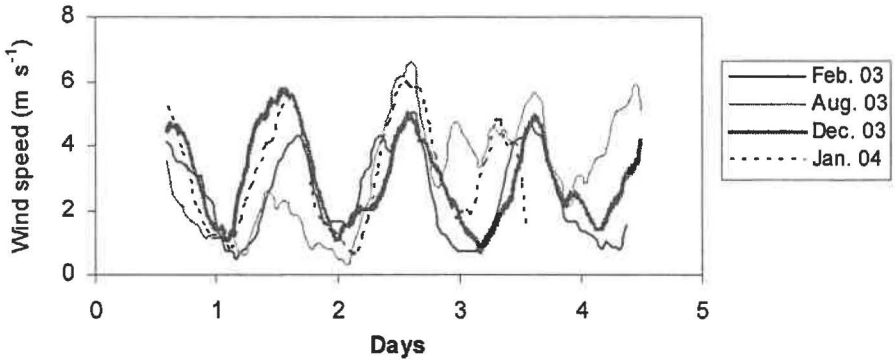

Figure 4.3: Mean hourly wind speed at 10 m elevation over the duration of each sediment trap deployment in Feb., Aug. and Dec. 2003, and Jan. 2004.

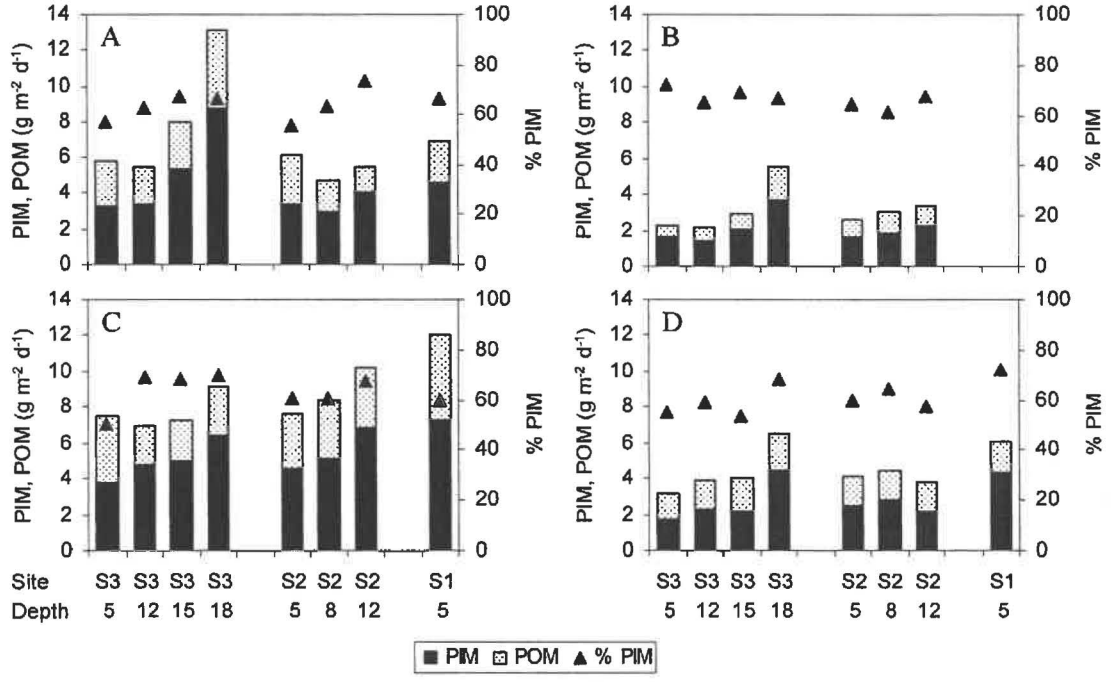

Figure 4.4: Gross sedimentation rates of particulate inorganic matter (PIM) and particulate organic matter (POM), and PIM as a percentage of total particulate material, for traps suspended at depths given in the horizontal axis label below the site labels, at sites S3, S2 and S1 for (A) Feb. 2003, (B) Aug. 2003, (C) Dec. 2003 and (D) Jan. 2004. There were no data for site 1 in Aug. 2003.

The fraction of TPM represented by inorganic material also increased with trapping depth at sites 2 and 3 for all deployments except August 2003 (Fig. 4.4).

At site 3, gross trapping rates of TN and TP also generally increased with trap depth, with the largest increase occurring for TP (Fig. 4.5). The mean increase in trapping rate between surface and bottom traps over the four deployments was 55 % for P and

31 % for N. This was reflected in the TN:TP molar ratio, which decreased between 29 and 40 % between surface and bottom traps at this site (Fig. 4.5). At site 2, TN:TP molar ratios also decreased between surface and bottom traps for all deployments, from 1 to 30 % for the four deployments (Fig. 4.5). At sites 2 and 3, the POC:PON molar ratio was relatively invariant between surface and bottom traps for the two incubations in which POC and PON were measured (Feb. 2003 and Jan. 2004, Fig. 4.6).

For the bottom-most traps, the fraction of TPM due to resuspension (f_r), was much higher at site 1 (mean 64 %) than at site 2 (mean 10 %) or site 3 (mean 36 %) (Table 4.2). At all sites, there was no relationship ($p > 0.05$) between f_r and mean wind speed calculated from hourly measurements over the duration of each deployment. No data were available for site 1 in August 2003 as sediment traps were not recovered.

Net sedimentation rates of TPM, chl-*a*, TN, TP, POC and PON, after correction for resuspension, were determined from traps positioned immediately above the bottom sediments at each site (Table 4.2). Mean sedimentation rate of TPM for all deployments was highest at site 3 (mean 5.6 g m^{-2} d^{-1}) followed by site 2 (5.0 g m^{-2} d^{-1}) and site 1 (3.3 g m^{-2} d^{-1}, Fig. 4.7) though differences between sites were not significant ($p > 0.05$, Table 4.3). In December 2003, mean sedimentation rates of TPM for the three stations were significantly higher ($p > 0.05$) than for any other period, coinciding with high chl-*a* fluorescence in bottom waters (Fig. 4.2). In August 2003 sedimentation rates at sites 2 and 3 were at least 1.5 times lower than during any of the other seasonal deployments.

Particulate organic material constituted between 28 and 31 % of TPM at site 3 over all periods (Table 4.2) while at sites 2 and 1, POM was much more variable, with a range of 14-89 % and 15-50 %, respectively. Chlorophyll *a* sedimentation rates across all sites ranged from 13 to 91 mg m^{-2} d^{-1} and were lowest in August 2003 and highest in January 2004 (site 3) or December 2003 (sites 1 and 2, Fig. 4.7). Rates in December 2003 were significantly higher than in August 2003 or January 2004 (Table 4.3). Mean chl-*a* sedimentation rates were highest at site 2 (mean 51 mg m^{-2} d^{-1}) followed by site 3 (47 mg m^{-2} d^{-1}) and site 1 (32 mg m^{-2} d^{-1}), although differences between sites were not statistically significant (Table 4.3). Sedimentation rates of TN

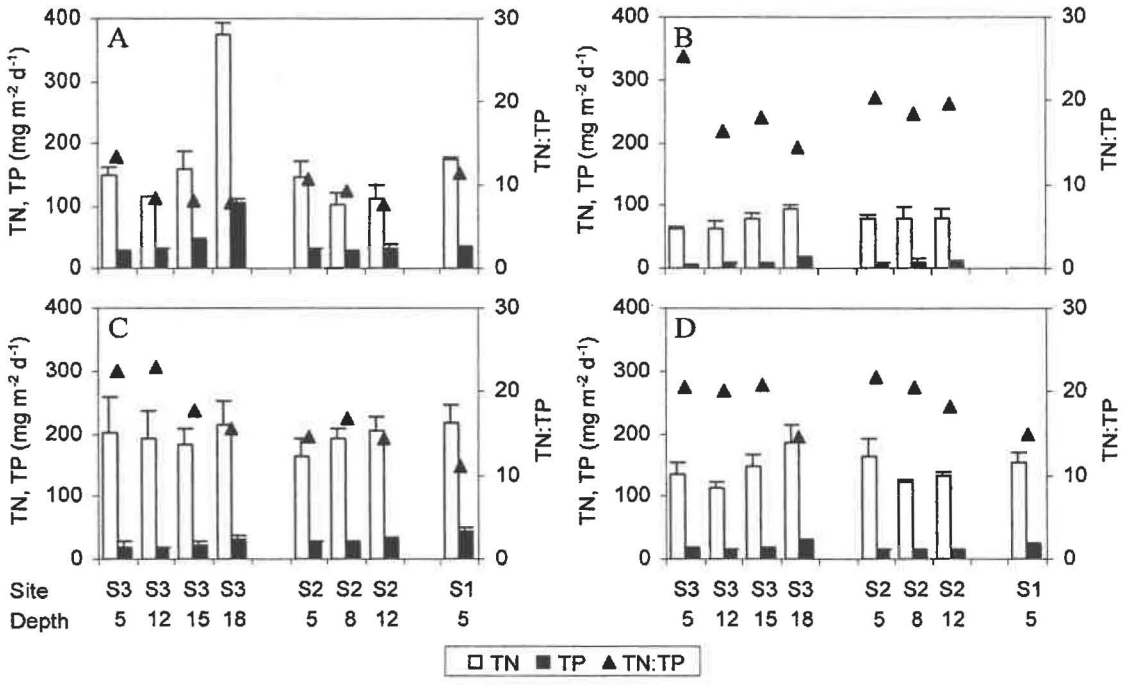

Figure 4.5: Gross sedimentation rates of total nitrogen (TN) and total phosphorus (TP), and TN:TP molar ratios, for traps suspended at depths given in the horizontal axis label below the site labels, at sites S3, S2 and S1 for (A) Feb. 2003, (B) Aug. 2003, (C) Dec. 2003 and (D) Jan. 2004. There were no data for site 1 in Aug. 2003. Error bars represent standard deviations.

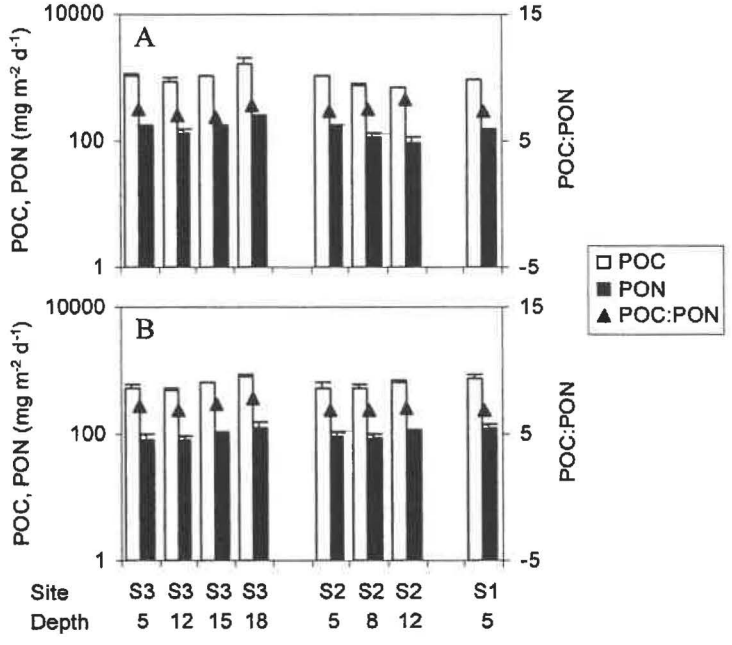

Figure 4.6: Gross sedimentation rates of particulate organic carbon (POC) and particulate organic nitrogen (PON), and POC:PON molar ratios, for traps suspended at depths given in the horizontal axis label below the site labels, at sites S3, S2 and S1 for (A) Feb. 2003 and (B) Jan. 2004. Error bars represent standard deviations.

Table 4.2: Net sedimentation rates of total particulate material (TPM), chlorophyll *a* (chl-*a*), total nitrogen (TN), total phosphorus (TP), particulate organic carbon (POC) and particulate organic nitrogen (PON), as measured in the bottom-most traps at each site. f_r and POM represent the fraction of TPM due to resuspension and particulate organic material, respectively. POC:PON (C:N) and TN:TP are molar ratios.

Site	Depth	Date	TPM	f_r	POM	chl-*a*	TN	TP	TN:TP	POC	PON	C:N
	m		g m^{-2} d^{-1}	%	%	mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	mg m^{-2} d^{-1}		mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	
1	7	Feb. 2003	2.1	69	33.3	32.6	22.7	10.5	4.8	295.1	46.7	7.4
		Dec. 2003	5.9	51	40.1	49.4	107.1	21.2	11.2			
		Jan. 2004	1.8	71	27.8	15.0	44.5	6.7	14.8	218.8	37.3	6.9
2	14	Feb. 2003	4.7	13.8	26.6	43.6	94.9	27.7	7.6	585.5	82.6	8.3
		Aug. 2003	3.0	10.1	32.7	24.0	70.6	8.0	19.6			
		Dec. 2003	8.4	17.3	32.7	91.3	169.6	25.9	14.5			
		Jan. 2004	3.7	0.0	42.5	43.8	129.6	15.7	18.2	627.2	103.1	7.1
3	20	Feb. 2003	8.0	39.0	30.7	79.9	228.2	64.7	7.8	1040.4	155.9	7.8
		Aug. 2003	3.0	46.7	28.2	13.1	50.9	7.8	14.4			
		Dec. 2003	7.3	19.8	29.6	56.8	170.8	24.3	15.5			
		Jan. 2004	4.0	37.8	29.9	39.6	114.9	17.4	14.6	499.2	74.8	7.8

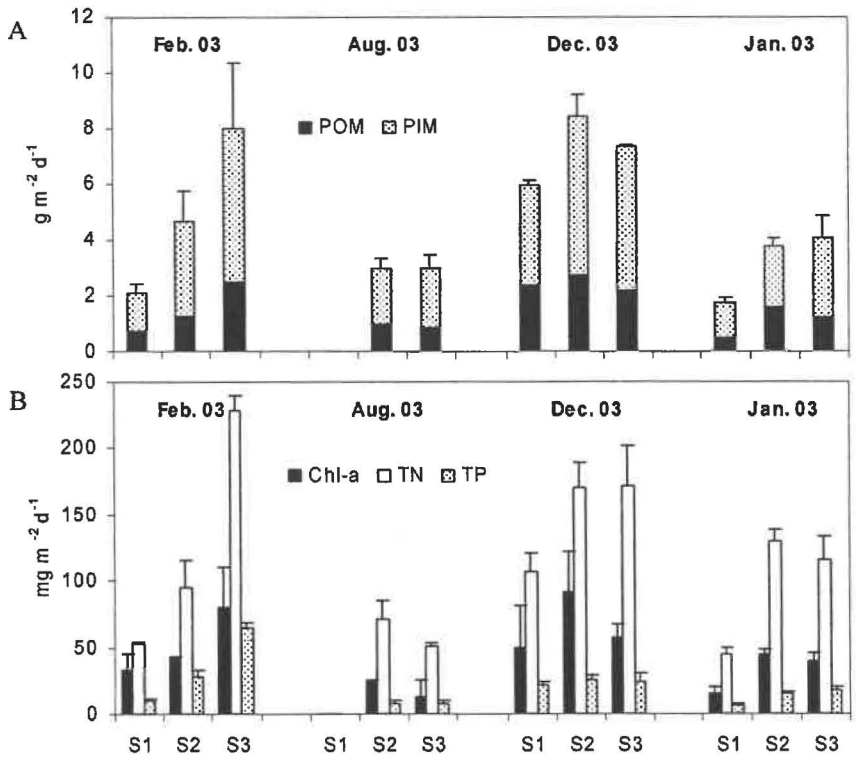

Figure 4.7: Net sedimentation rates of (A) particulate inorganic matter (PIM) and particulate organic matter (POM) and (B) chlorophyll *a* (chl-*a*), total nitrogen (TN) and total phosphorus (TP) at sites S1, S2 and S3 for Feb., Aug. and Nov. 2003, and Jan. 2004. Error bars represent standard deviations.

Table 4.3: Summary of one way ANOVA for site or period, for net sedimentation rates of total particulate matter (TPM), chlorophyll *a* (chl-*a*), total nitrogen (TN) and total phosphorus (TP). df is degrees of freedom, MS is mean square, F is the test statistic and p is probability.

		Site				Period				
Variable	**Factor**	**df**	**MS**	**F**	**p**	**Factor**	**df**	**MS**	**F**	**p**
TPM	Site	2	14.3	2.76	0.080	Period	3	32.0	10.56	< 0.001
	Error	30	5.2			Error	29	3.0		
chl-a	Site	2	1900.6	2.52	0.102	Period	3	3081.7	5.59	0.005
	Error	24	755.6			Error	23	551.7		
TN	Site	2	16675.1	6.53	0.005	Period	3	8776.3	2.95	0.054
	Error	24	2554.9			Error	23	2971.3		
TP	Site	2	454.2	2.20	0.132	Period	3	800.2	5.33	0.006
	Error	24	206.1			Error	23	150.2		

ranged from 23 to 228 mg m^{-2} d^{-1} across the three sites and four deployment periods (Table 4.2). Mean rates over all periods were highest at site 3 (142 mg m^{-2} d^{-1}) followed by sites 2 and 1 (116 and 68 mg m^{-2} d^{-1}, respectively, Fig. 4.7), although differences between sites were not statistically significant (Table 4.3). Rates of TP sedimentation ranged from 7 to 65 mg m^{-2} d^{-1} and were significantly higher ($p < 0.05$) at site 3 (mean 29 mg m^{-2} d^{-1}) than at site 1 (mean 13 mg m^{-2} d^{-1}) over all periods, with intermediate levels at site 2 (mean 19 mg m^{-2} d^{-1}) (Table 4.3). There were no significant differences ($p > 0.05$) in TP sedimentation rates between periods. The mean molar ratio of TN:TP was 13.6 over all sites and all periods. Sedimentation rates of POC and PON ranged from 219 to 1040 and 37 to 156 mg m^{-2} d^{-1}, respectively (Table 4.2). In February 2003 the highest sedimentation rates for both POC and PON were at site 3 while in January 2003, the highest rates were at site 2 (Fig. 4.8). The mean C:N molar ratio was 7.6 over all sites for the two sample periods of February 2003 and January 2004.

Rates of TPM sedimentation were not significantly correlated ($P > 0.05$, Pearson's correlation coefficient) with vertically integrated chlorophyll fluorescence in the surface-mixed layer (0-8 m) over all sites and periods. Sedimentation rates of TPM were also not significantly correlated with mean wind speed, or water column TPM and chl-*a* concentrations.

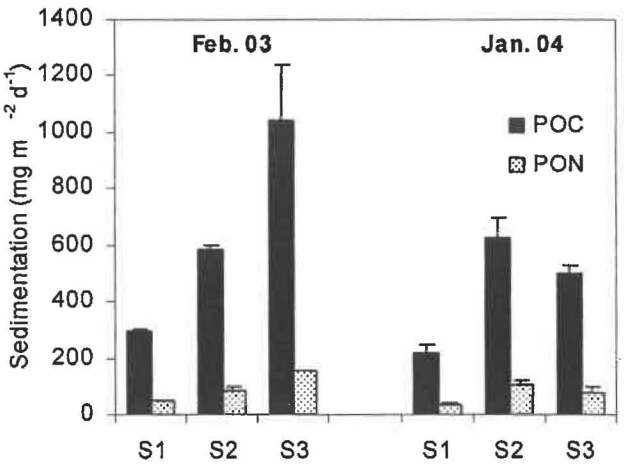

Figure 4.8: Sedimentation rates of particulate organic carbon (POC) and particulate organic nitrogen (PON) at sites S1, S2 and S3 in Feb. 2003 and Jan. 2004. Error bars represent standard deviations.

4.4 Discussion

4.4.1 Sediment resuspension

Sediment resuspension is an important component of the sedimentation of TPM in Lake Rotorua. Sedimentation fluxes were characterised by increases in fractions of PIM and decreases in TN:TP molar ratios with increased trap depth at individual stations, which were driven mostly by dominance of mineral-bound P in association with sediment resuspension (e.g., Hamilton and Mitchell, 1996). Molar ratios of POC:PON were relatively invariant with depth, suggesting that mineralisation of organic matter in the water column was not a major contributor to the transitions of organic and inorganic fractions with depth in the traps.

Estimates of the proportion of sedimenting material derived from resuspension were up to 71 %, with the upper limit similar to that reported for other lakes of similar depth and trophic status (Weyhenmeyer et al., 1995; Koski-Vähälä, 2000). Sediment resuspension is influenced primarily by wind speed and direction, as well as lake size, morphology and water depth (Bloesch, 1995). In this study, estimates of resuspension were not significantly correlated with wind speed, at least partly because daily mean wind speed values of c. 3 m s^{-1} were similar between the four deployments. However, large variations in hourly wind speed measurements within individual deployments suggest that daily rather than seasonal variability may be more important for

resuspension events, and that the four-day deployment time used in this study was too long to capture these differences.

In Lake Rotorua, 34 % of the total lake area has a water column depth less than 7 m, suggesting that potential lake-wide effects of resuspension may be substantial. High values of resuspension of inorganic material at shallow site 1 are indicative of near-shore resuspension by surface waves. At sites 2 and 3, where the effects of surface waves are unlikely to exceed critical thresholds for resuspension (e.g. Bloesch, 1994), resuspended material in bottom traps is most likely derived from horizontal transport of resuspended material from shallower regions. The contribution of resuspension to the annual nutrient load is difficult to quantify from the results obtained in this study as it is not known how often material is repeatedly resuspended before final burial in the sediments. However, Lowe et al. (2001) and Jeppesen et al. (2003) suggest that resuspension does not necessarily delay the recovery of large lakes after a reduction in external nutrient loading.

4.4.2 Sedimentation rates

Sedimentation rates of TPM in Lake Rotorua, corrected for resuspension, were in the range 1.8 to 8.2 g m^{-2} d^{-1}, which is similar to that reported for other eutrophic lakes (Koski-Vähälä, 2000; Chalar and Tundisi, 2001). Sedimentation rates in the lake demonstrated a clear seasonality, with higher values generally observed during summer trap deployments when water column chl-*a* concentrations were highest. However, relationships of sedimentation rate with chl-*a* concentrations or fluorescence in the surface-mixed layer (depth integrated 0-8 m) were not statistically significant. In other studies, relationships between sedimentation rates and phytoplankton biomass or chl-*a* concentrations have been reported as both not significant (e.g. Koski-Vähälä et al., 2000; García-Ruiz et al., 2001) and significant (Guy et al., 1994; Kleeberg, 2002).

Material sedimenting in Lake Rotorua has a high TP and TN content (mean 4.2 mg P g TPM $^{-1}$ and 22.8 mg N g TPM $^{-1}$) relative to values given in the literature of 1 to 2.7 mg P g TPM $^{-1}$ and 8.1 to 13 mg N g TPM $^{-1}$ (Nõges et al., 1999; Koski-Vähälä et al., 2000; Chalar and Tundisi, 2001; Kleeberg, 2002). While the sedimenting organic fraction represented only 32 % of TPM over all sites and deployments, it appeared to

be highly enriched in nutrients. The N:P molar ratio of trap material of approximately 16 is consistent with what would be expected for phytoplankton deposition (Redfield, 1958), except during February 2003. During this period, mean molar N:P ratios were 6.8 and POC:PON ratios were 7.8 over the three sites, indicating that the depositional material was enriched in P, possibly in association with sediment P release (Burger et al., 2005) or with elevated phytoplankton cellular P concentrations associated with luxury uptake of P.

4.4.3 Contribution to internal loading

From a mass balance for nutrients in Lake Rotorua, Beyá et al. (2005) estimate net retention of 2.1 mg TP m^{-2} yr^{-1} and 25.6 mg TN m^{-2} yr^{-1} in the bottom sediments. These values are 4-fold lower than the mean net TN sedimentation rate, and 10-fold lower than the mean net TP sedimentation rate over all periods and sites in our study. The difference between the two studies may be attributed to continuity of recycling between the water column and bottom sediments, and suggests that N and P are recycled many times between the sediments and water column before they are ultimately lost from the system. The much greater difference in estimates of retention and actual measurements for phosphorus compared with nitrogen may suggest that denitrification is also an important process in loss of nitrogen in this lake.

The high rates of net particulate nutrient sedimentation observed in Lake Rotorua may have important implications for management of eutrophication in the lake, and suggest that improvements in lake water quality will be delayed after reductions in external nutrient loads. High rates of organic matter sedimentation and subsequent decomposition at the sediment-water interface may be important for enhancing sediment release rates of N and P back into the water column under certain environmental conditions (Gächter et al., 1988; Marsden, 1989). Furthermore, resuspension processes may also be important for directly remobilising dissolved nutrients from the sediment porewaters back into the overlying water column (Søndergaard, 1992).

Our study suggests that the development of management strategies, where internal loading is important, needs to be developed in the context of the extent of nutrient recycling. Furthermore, it highlights the importance of conducting experimental

measurements of sedimentation rates and other sediment nutrient fluxes that contribute to the internal nutrient cycle, such as sediment nutrient release and sediment resuspension, as opposed to the use of estimations derived from simple mass balance equations.

4.6 References

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Chapter 5: Benthic nutrient fluxes in Lake Rotorua[1]

Abstract

Sediment release rates of soluble reactive phosphorus (SRP) and ammonium (NH_4) were determined seasonally at three sites (water depth 7, 14 and 20 m) in Lake Rotorua using *in situ* benthic chamber incubations. Release rates of SRP ranged from 2.2 to 85.6 mg P m^{-2} d^{-1} and were largely independent of dissolved oxygen (DO) concentration. Two phases of NH_4 release were observed in the chamber incubations; high initial rates of up to 2200 mg N m^{-2} d^{-1} in the first 12 h of deployment followed by lower rates of up to 270 mg N m^{-2} d^{-1} in the remaining 36 h of deployment. Releases of SRP and NH_4 were highest in summer and at the deepest of the three sites. High organic matter supply rates to the sediments may be important for sustaining high rates of sediment nutrient release. A nutrient budget of Lake Rotorua indicates that internal nutrient sources derived from benthic fluxes are more important than external nutrient sources to the lake.

5.1 Introduction

Sediment fluxes of nitrogen (N) and phosphorus (P) to the overlying water column may support a significant fraction of the total nutrient requirements for primary productivity in lotic systems (Marsden, 1989; Søndergaard et al., 1999). Prolonged external loading may ultimately produce elevated levels of nutrients in bottom sediments that, under certain environmental conditions such as anoxia, are remobilised and returned to the water column (Boström et al., 1988). Thus sustained high concentrations of water column nutrients have been observed in many lakes despite large reductions in external loads, particularly from point source inputs (Marsden, 1989; Søndergaard et al, 2003). Studies of lake nutrient cycling, particularly in the Northern Hemisphere, emphasise P release because of its impact on phytoplankton production (e.g., Kleeberg and Kozerski, 1997; Søndergaard et al.,

[1] Accepted for publication in *Hydrobiologia* as: D.F. Burger, D.P. Hamilton, C. A. Pilditch and M. M. Gibbs: Benthic nutrient fluxes in a eutrophic, polymictic lake.

2003). However, N can also limit or co-limit phytoplankton growth (White et al., 1986; Philips et al., 1997; Hameed et al., 1999), and may be as common as P limitation (Elser et al., 1990). Quantification of sediment N and P fluxes and their contribution to the total nutrient load is therefore important in eutrophic lakes and is a prerequisite to targeted nutrient management and lake restoration programmes.

Sediment nutrient release rates are mediated by interactions of many physical, chemical and biological processes (Boström et al., 1988). Factors influencing P include desorption and dissolution of P bound to iron, manganese and other inorganic complexes under reducing conditions (Mortimer, 1941; 1942), molecular diffusion from sediment porewaters to the water column along steep concentration gradients (Boström et al., 1988; Søndergaard, 1989), and mineralisation of organic material by bacteria (Gächter et al., 1988; Marsden, 1989). Sediment resuspension may also mediate P release by entrainment of sediment porewaters (Søndergaard, 1992). Nitrogen release from bottom sediments occurs predominantly as ammonium (NH_4), as a result of particulate organic matter decomposition by bacterial mineralisation (Forsberg, 1989). Autolysis or hydrolysis of organic material leads to the production of dissolved organic N, which may be further mineralised to NH_4 via bacterial deamination (Hargreaves, 1998). Ammonium may be further oxidised to nitrate if the bottom sediments are well oxidised (Hargreaves, 1998; Beutel, 2001).

Direct measurements of sediment nutrient release rates are generally obtained from sediment core incubations conducted in the laboratory (e.g. Boström and Pettersson, 1982; Nürnberg, 1987; Jensen et al., 1992; Krivtsov et al., 2001). Incubations typically incorporate only a small sediment area (< 0.01 m^{-2}), but allow for tight environmental controls and provide opportunities to manipulate cores to address specific questions. Removal of cores from the lake may also alter the physical, chemical and biological characteristics of the sediments through sediment re-oxygenation, porewater displacement, loss of the benthic boundary layer, and changes in temperature and light regimes. The use of benthic chambers allows nutrient fluxes to be determined *in situ* with minimal disturbance to the sediments and overlying water (see review by Tengberg et al., 1995), while incorporating a large sediment surface area as well as the natural light and temperature conditions of the lake.

The primary objective of this study was to quantify seasonal and spatial variations in sediment release of NH_4 and soluble reactive phosphorus in eutrophic, polymictic Lake Rotorua, using *in situ* benthic chamber deployments. A further objective was to use this information to provide comparisons between the magnitude of internal and external nutrient loads to the lake, so that an understanding could be developed of the effects and response time related to catchment management actions.

5.1.1 Study site

Lake Rotorua is a large (79.8 km^2), shallow (mean depth 10.8 m), polymictic lake in central North Island, New Zealand (Fig. 5.1). The lake is eutrophic (Rutherford et al., 1996) and annual mean water column concentrations of total phosphorus (TP) and total nitrogen (TN) are 0.055 mg L^{-1} and 0.814 mg L^{-1}, respectively. The Lake Rotorua catchment area of 425 km^2 is dominated by agriculture (48 %) and plantation forestry (23 %). There are nine major inflows to the lake (mean discharge 0.22-2.75 m^3 s^{-1}) as well as 17 minor inflows, including urban drains and geothermal springs (mean discharge < 0.06 m^3 s^{-1}). Until 1991 Lake Rotorua received discharges of wastewater from Rotorua city (population 60,000), which contributed annual nutrient loads of 35 tonnes TP yr^{-1} and 150 tonnes TN yr^{-1} (White et al., 1992). While removal of wastewater discharges was expected to improve lake water quality (Rutherford, 1996), water column nutrient concentrations have remained high, coinciding with frequent summer blooms of cyanobacteria during summer months.

5.2 Methods

5.2.1 Sediment nutrient fluxes

Benthic chambers were deployed at three sites (Fig. 5.1) on four occasions between February 2003 and January 2004 (Table 5.1). Sites were chosen to reflect the natural variability in mixing regime, from permanently well mixed and oxygenated in shallow regions (site 1: depth 7 m), to periodically stratified and anoxic in deeper regions (site 2: depth 14 m and site 3: depth 20 m). At sites 1 and 2 both light chambers (circular, 6 mm acrylic plastic, encompassing sediment area 0.111 m^2 and water volume 17.8 L) and dark chambers (circular, 8 mm PVC, encompassing sediment area 0.116 m^2 and water volume 18.5 L) were deployed in duplicate. At site 3 (depth 20 m), where light at the sediment surface was < 1% of photosynthetically

available radiation (PAR) at the water surface (Table 5.1), only light chambers were deployed. Two chambers were deployed at site 3 in all periods except February 2004, when four chambers were used.

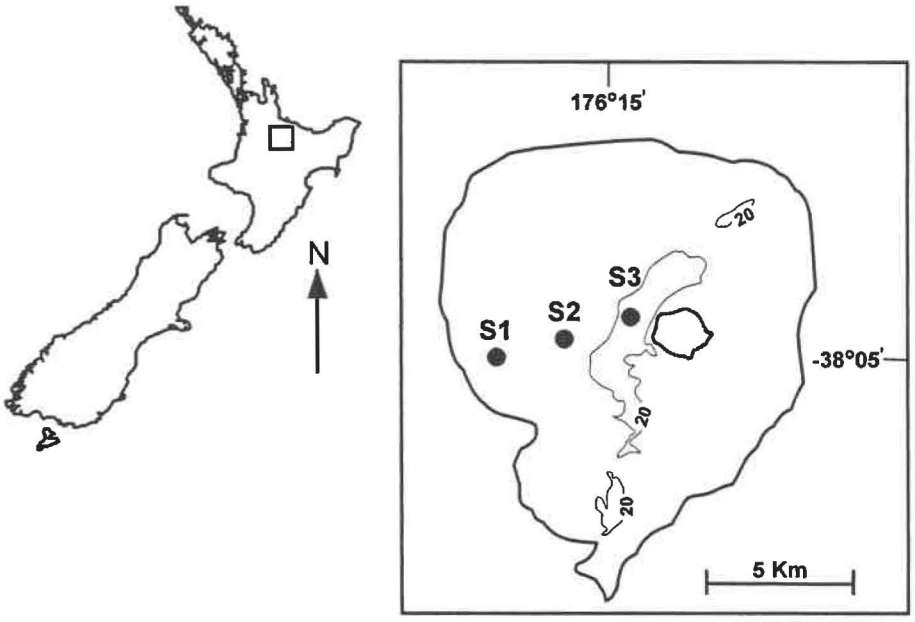

Figure 5.1: Map of Lake Rotorua showing chamber deployment sites: Site 1 (S1, depth 7 m), Site 2 (S2, depth 14 m) and Site 3 (S3, depth 20 m). The 20-m depth contour is also shown.

On each sampling date, chambers were deployed between 0830 and 1400 h, depending on weather conditions. Deployment was assisted by SCUBA divers to minimise sediment disturbance during insertion of the chambers into the sediments. Chambers were pushed into the sediments to a depth of 80 mm, corresponding to the position of a flange on the outside of each chamber. After chamber insertion, taps (Ø = 9 mm) in the chamber lids were left open for 20 mins before the start of each experiment. Water in the chambers was mixed throughout the experiment with a submersible 6 V DC pump (LVM Ltd), which circulated for 5 s each minute. Laboratory trials showed that this flow regime maintained well-mixed conditions inside the chambers without inducing sediment resuspension. Bottom water samples were also collected during all deployments, and incubated in duplicate dark and light 1 L PET® bottles alongside the chambers, to measure water column nutrient regeneration rates in the absence of bottom sediments.

Chambers were sampled four times daily, depending on incubation start time and weather conditions; usually at 0700, 1100, 1500 and 1900 h, over 2 days. This deployment period was sufficient to create anoxic conditions in the chambers at sites 2 and 3 during summer incubations, thereby simulating release rates normally observed during natural stratification events when bottom waters become anoxic (Burger et al., 2005). Water was transported from the chambers to the surface under reduced pressure through clear plastic tubing (Ø = 4 mm) and collected in an in-line trap after flushing each line. A small external opening (Ø = 4 mm) in the chamber lid allowed replenishment of water sampled from the chamber with water from the depth of deployment.

A sample volume of up to 60 mL was collected from each chamber on each sampling occasion, of which 25 mL was immediately separated for analysis of dissolved oxygen (DO) concentration (YSI Instruments, Model 50, probe electrode model 5739). The remaining sample was filtered through GF/C 25 mm diameter syringe filters and placed on ice before return to the laboratory, where filtrate was frozen before analysis for NH_4, NO_3 and SRP on a Lachat Instruments flow injection analyser (FIA, Zellweger Analytics, 2000). On three sampling occasions (Aug. and Nov. 2003, and Jan. 2004), *in situ* DO sensors (Van Essen Instruments) were also used to record changes in DO concentration at 15 minute intervals in a light and a dark chamber (sites 1 and 2) or in all chambers (site 3).

Sediment NH_4 and SRP fluxes were calculated from the slope of linear regressions of chamber nutrient concentrations with time (Gibbs et al., 2002). After correcting for the effect of dilution associated with sample removal, rates of changing nutrient concentrations in the chamber were divided by the sediment surface area in the chambers to give an aerial release rate. Changes in nutrient concentrations in control bottles incubated alongside the chambers during each deployment were < 0.020 and < 0.006 mg L d^{-1} for NH_4 and SRP, respectively, and were subtracted from the final sediment release rate. Fluxes of NO_3 were not calculated as concentrations in the chambers were less than 5 % of those of NH_4 and were often below analytical detection limits (0.001 mg L^{-1}). Where *in situ* DO sensors were deployed inside the chambers, sediment oxygen demand (SOD) was calculated from the slope of linear regressions of chamber DO concentrations over the time period 0.25 to 2.25 h. For

remaining deployments, SOD was calculated from the rate of change of DO between the first and second measurements (i.e. c. 4 h).

Differences in SRP and NH_4 release rates and SOD between sites, period, and sites x period were examined using a two-way analysis of variance (ANOVA) with *post-hoc* analysis using the Tukey HSD test with a confidence interval of 95 %. Prior to ANOVA analysis, data were examined for normality and homogeneity of variance by visual inspection of residuals and no transformations were necessary.

5.2.2 Chamber water displacement

Rates of water dilution in each chamber were assessed on one sampling occasion (Feb. 2003) by injecting the chambers with a bromine tracer (LiBr at 5 $\mu g\ L^{-1}$) at the start of each deployment, and measuring changes in Br concentration at 0.5 and 48 hours. Concentrations of Br were analysed by mass spectroscopy and varied little (< 0.003 μg Br L^{-1}) from the dilution rate calculated using the total volume of water displaced from each chamber during sampling. Groundwater flows were also assessed using observations by divers of water bladders placed on the chamber outlet for 20 mins at 48 h during the same deployment. The bladders did not inflate, indicating that groundwater influxes were likely to be low.

5.2.3 Water column measurements

Vertical profiles of conductivity-temperature-depth (CTD) profiles (Seabird Electronics) with an additional CTD-mounted sensor for DO concentration and PAR were taken at the start of each deployment and during subsequent collection of nutrient samples from the chambers. Concentrations of NH_4, NO_3 and SRP were determined on bottom water samples collected with a Schindler-Patalas trap at the start of each deployment. Further samples for nutrient analysis were collected daily at each site during the chamber incubations.

5.3 Results

5.3.1 Water column variables

Water column profiles of temperature and DO concentration, collected from each site at the start of the four chamber incubations, are shown in Fig. 5.2. The water column

was thermally stratified at sites 2 and 3 in February 2003 (summer) and again in January 2004. The mean thermocline depth (dp/dz = minimum) on these two occasions was between 7 and 8 m, with a temperature difference of 2 °C between surface and bottom waters (Fig. 5.2). Stratification was accompanied by reduced DO concentrations in the hypolimnion during both periods, particularly at site 3 (< 3.6 mg L^{-1}, Fig. 5.2, Table 5.1). During August (winter) and November (late spring) 2003, the water column was isothermal at all sites, and DO concentrations were nearly homogeneous and close to saturation. Mean bottom water temperatures across all sites during each chamber deployment were highest in January 2004 (20.8 °C) and lowest in August 2003 (13.2 °C, Table 5.1).

Bottom water concentrations of NH_4, SRP and NO_3, corresponding to initiation of each chamber deployment, varied between seasons and sites (Table 5.1). Mean concentrations of SRP over all seasons were highest at site 3 (0.042 mg L^{-1}) followed by site 2 and site 1 (0.022 and 0.018 mg L^{-1}, respectively). Nutrient concentrations in bottom waters were lowest in August 2003 and highest in February 2003, when DO concentrations were low. Mean concentrations of NH_4 were also highest at site 3 (0.184 mg L^{-1}), followed by sites 2 and 1 (0.171 mg L^{-1} and 0.053 mg L^{-1}, respectively). Mean concentrations of NO_3 over the four periods were highest at site 1 (0.012 mg L^{-1}) and lowest at site 2 (0.008 mg L^{-1}). Over all periods, mean values of PAR at the depth of the chamber incubations at each site were highest at site 1 (mean 5.12 µmol quanta m^{-2} s^{-1}) followed by site 2 (0.19 µmol quanta m^{-2} s^{-1}) and site 3 (0.10 µmol quanta m^{-2} s^{-1}, Table 5.1).

5.3.2 Sediment oxygen demand

Sediment oxygen demand (SOD) ranged from 0.3 g m^{-2} d^{-1} (site 2, Aug. 2003) to 4.0 g m^{-2} d^{-1} (site 3, Nov. 2003, Table 5.2). Mean SOD calculated over all periods was highest at site 3 (mean 1.9 g m^{-2} d^{-1}) followed by site 2 (mean 1.5 g m^{-2} d^{-1}) and site 1 (mean 0.9 g m^{-2} d^{-1}) (Table 5.2). Values of SOD at sites 2 and 3 were low in February 2003 and 2004, partly due to reduced initial DO concentrations associated with stratification (Fig. 5.2). At sites 1 and 2, differences in mean SOD between light and dark chambers were low (< 0.3 g m^{-2} d^{-1}), except at site 1 in November 2003 when SOD was nearly five times higher in the dark chambers than in the light chambers ($P < 0.01$) (Table 5.2).

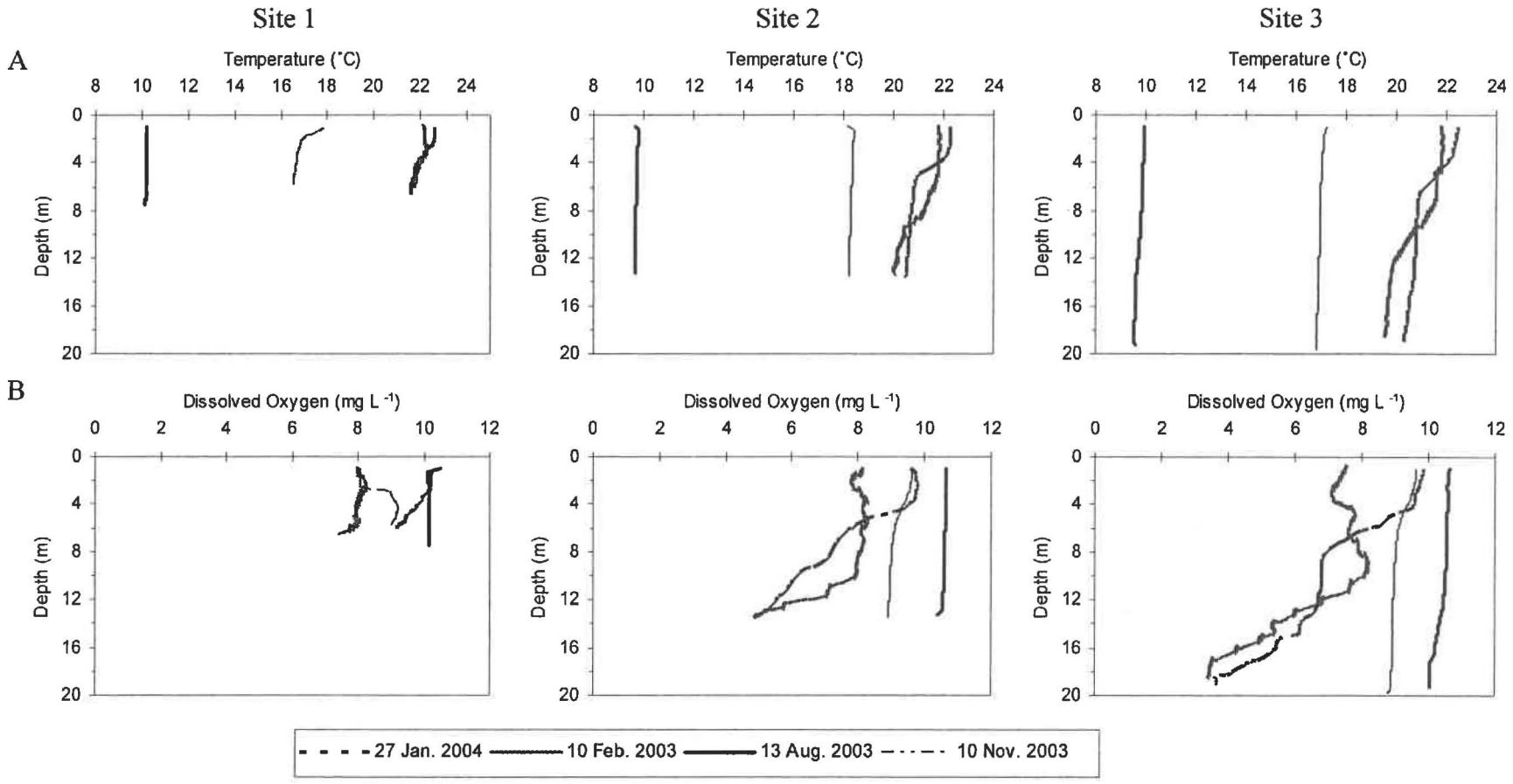

Figure 5.2: Water column profiles of (A) temperature and (B) dissolved oxygen concentration at sites 1, 2 and 3 on 10 Feb., 13 Aug. and 10 Nov. 2003, and 27 Jan. 2004.

Table 5.1: Mean concentrations of ammonium (NH_4), soluble reactive phosphorus (SRP), nitrate (NO_3) and dissolved oxygen (DO) in bottom waters at sites 1, 2 and 3 at the start of each incubation. Temperature (T) and photosynthetically available radiation (PAR) are mean values in bottom waters derived from daily CTD casts during each chamber deployment.

Site	Date	NH_4	SRP	NO_3	DO	T	PAR
		mg L^{-1}	mg L^{-1}	mg L^{-1}	mg L^{-1}	°C	µmol quanta m^{-2} s^{-1}
1	10 Feb. 2003	0.097	0.017	0.015	7.5	21.7	4.31
	13 Aug. 2003	0.037	0.011	0.015	10.2	10.2	9.19
	10 Nov. 2003	0.023	0.020	0.011	9.0	16.5	6.53
	27 Jan. 2004	0.056	0.024	0.007	8.5	21.8	0.45
2	10 Feb. 2003	0.187	0.027	0.015	4.9	20.1	0.09
	13 Aug. 2003	0.049	0.010	0.008	10.5	9.7	0.44
	10 Nov. 2003	0.037	0.023	0.004	8.9	18.2	0.12
	27 Jan. 2004	0.413	0.029	0.004	6.7	20.4	0.11
3	10 Feb. 2003	0.374	0.055	0.010	3.4	19.5	0.10
	13 Aug. 2003	0.040	0.015	0.005	9.1	9.6	0.09
	4 Nov. 2003	0.058	0.015	0.005	8.9	16.8	0.08
	27 Jan. 2004	0.263	0.081	0.015	3.6	20.3	0.12

Table 5.2: Mean sediment release rates for ammonium from 0 to 12 h (NH_4 1) and 12 to 48 h (NH_4 2), and soluble reactive phosphorus (SRP, 0-48 h), as well as sediment oxygen demand rate (SOD) obtained with light and dark benthic chambers on four occasions between Feb. 2003 and Jan. 2004. Note: dark chambers were not used at site 3.

			Light chambers				Dark chambers			
Site	Period	n	NH_4 1	NH_4 2	SRP	SOD	NH_4 1	NH_4 2	SRP	SOD
			mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	g m^{-2} d^{-1}	mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	mg m^{-2} d^{-1}	g m^{-2} d^{-1}
1	10 Feb. 2003	2	414.6	70.3	10.2	0.75	415.5	109.2	6.5	0.80
	13 Aug. 2003	2	43.8	48.8	2.1	0.49	57.6	70.5	2.3	0.70
	10 Nov. 2003	2	190.9	81.8	5.8	1.09	278.6	84.3	5.4	5.14
	27 Jan. 2004	2	230.0	168.8	12.9	1.16	266.5	283.4	13.8	1.36
2	10 Feb. 2003	2	578.2	80.1	9.0	1.73	1320.8	188.2	29.4	1.63
	13 Aug. 2003	2	60.7	32.6	3.8	0.33	237.1	105.4	6.3	0.49
	10 Nov. 2003	2	95.6	59.7	11.5	0.67	563.7	67.4	4.2	1.42
	27 Jan. 2004	2	351.4	75.1	12.7	3.23	375.2	34.9	10.6	3.83
3	10 Feb. 2003	2	1957.8	223.9	85.6	1.75				
	13 Aug. 2003	2	93.5	52.8	5.6	1.26				
	4 Nov. 2003	2	2212.8	94.5	55.3	3.95				
	27 Jan. 2004	4	484.5	172.8	30.7	0.67				

5.3.3 SRP benthic fluxes

Concentrations of SRP in the light chambers increased in a relatively linear manner over time (Fig. 5.3) and the rate of release did not show an obvious dependence on DO concentrations inside the chambers. Linear regressions between SRP concentrations versus time for all sites and periods yielded a mean R^2 of 0.93 (range 0.82-0.99). Sediment SRP release rates ranged between 2.1 and 85.6 mg m^{-2} d^{-1} (Table 5.2, Fig. 5.4).

Statistical analyses showed highly significant effects of site ($P < 0.01$), period ($P < 0.01$) and site x period ($P < 0.01$) for sediment SRP releases (Table 5.3). *Post-hoc* analyses revealed release rates at site 3 (mean 44.3 mg m^{-2} d^{-1}) were significantly higher than release rates at site 2 (mean 9.3 mg m^{-2} d^{-1}) and site 1 (mean 7.7 mg m^{-2} d^{-1}) for all periods except August 2003 (Tables 5.2 and 5.3, Fig. 5.4). Release rates at site 3 were also significantly different between periods ($P < 0.01$), and were highest in February 2003 and lowest in August 2003. The observed rate in August 2003 was nearly 10 times lower than in all other periods (Table 5.2). At sites 1 and 2, SRP release rates were highest in January 2004 and lowest in August 2003 but were not significantly different between periods ($P > 0.05$). Differences in SRP release rates between light and dark chambers at site 1 were < 3.7 mg m^{-2} d^{-1} (Table 5.2, Fig. 5.5), and were not statistically significant (Table 5.4). In February 2003, SRP release rates at site 2 were three times higher in dark chambers (29.4 mg m^{-2} d^{-1}) than in light chambers (9 mg m^{-2} d^{-1}, Fig. 5.5).

5.3.4 NH_4 benthic fluxes

NH_4 fluxes were characterised by two rates of release (Fig. 5.3). The first phase from 0-12 h of deployment had a very high release rate, with maximum values in the light chambers of 415, 578 and 2213 mg m^{-2} d^{-1} at sites 1, 2 and 3, respectively (Fig. 5.3). In the second phase NH_4 release was substantially lower, with a maximum value across all sites of 224 mg m^{-2} d^{-1} (Fig. 5.3).

For initial rates of NH_4 release, there was a significant effect of site ($P < 0.01$), period ($P < 0.01$) and site x period ($P < 0.01$) (Table 5.3). Initial NH_4 fluxes at site 3 (mean 1187 mg m^{-2} d^{-1}) were significantly higher ($P < 0.05$) than at site 2 (mean 272 mg m^{-2} d^{-1}) and site 1 (mean 20 mg m^{-2} d^{-1}) (Tables 5.2 and 5.3, Fig. 5.4). Release rates

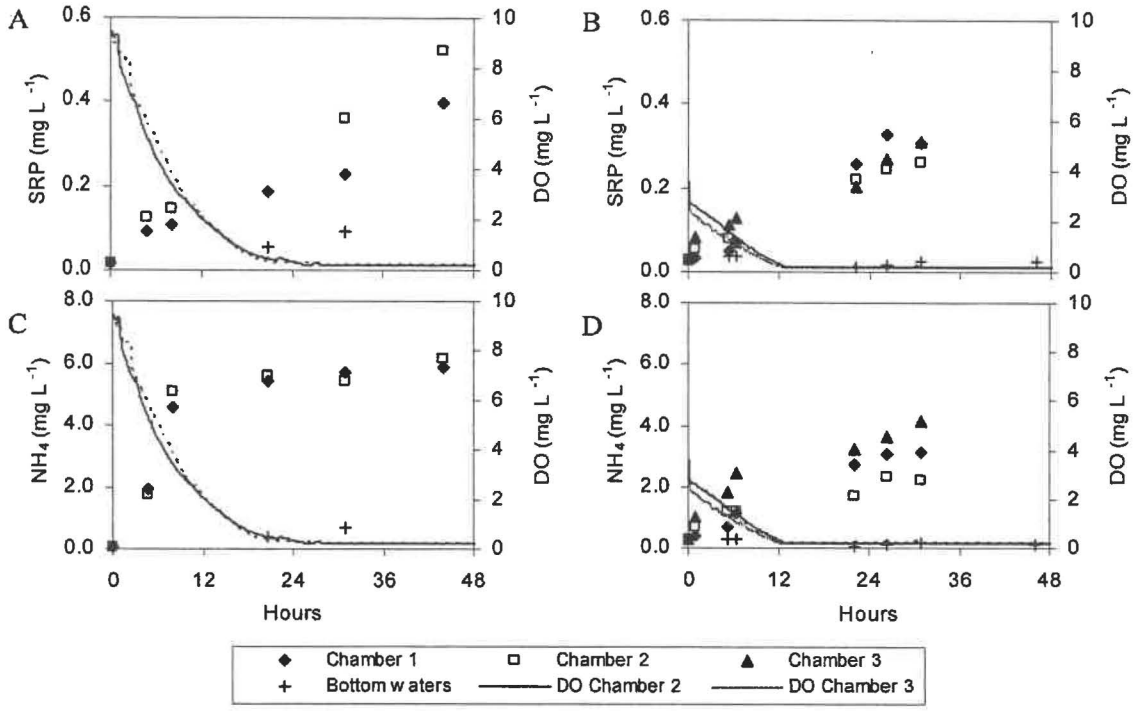

Figure 5.3: Changes in concentrations of phosphorus (SRP), ammonium (NH_4), and dissolved oxygen (DO) in replicate benthic chambers and bottom waters at site 3 in Nov. 2003 (A, C) and Jan. 2004 (B, D).

Table 5.3: Two-way analysis of variance between site, period and site x period for fluxes of soluble reactive phosphorus (SRP), ammonium in the phase 0 to 12 h (NH_4 1) and subsequent phase 12 to 48 h (NH_4 2). df is degrees of freedom, MS is mean squares, F is the test statistic and p is probability.

Fluxes	Factor	df	MS	F	p
SRP	Site	2	1554	58.07	< 0.01
	Period	3	656	24.51	< 0.01
	Site x Period	6	336	12.58	< 0.01
	Error	13	27		
NH_4 1	Site	2	2797711	201.37	< 0.01
	Period	3	887278	63.86	< 0.01
	Site x Period	6	740314	53.29	< 0.01
	Error	13	13893		
NH_4 2	Site	2	11650	5.09	0.023
	Period	3	11625	5.08	0.015
	Site x Period	6	3554	1.55	0.238
	Error	13	2291		

between sites 1 and 2 were not significantly different. At all sites, release rates were significantly lower in August 2003 than in all other periods. Release rates at sites 1 and 2 were highest in February 2003 and at site 3 in November 2003. The secondary

release rate of NH_4 was also highest at site 3 in all four deployments (mean 136 mg m^{-2} d^{-1}), followed by site 1 (mean 92 mg m^{-2} d^{-1}) and site 2 (mean 62 mg m^{-2} d^{-1}, Table 5.2, Fig. 5.5). Factorial analysis of variance ($P < 0.05$) showed an effect of site and period, but not site x period (Table 5.3). Values of NH_4 release at site 3 were significantly different from site 2 over all periods. At site 1, there was no significant difference between light and dark chambers for both phases of NH_4 release. At site 2, initial rates of NH_4 release were significantly higher ($P < 0.05$) in dark chambers than in light chambers.

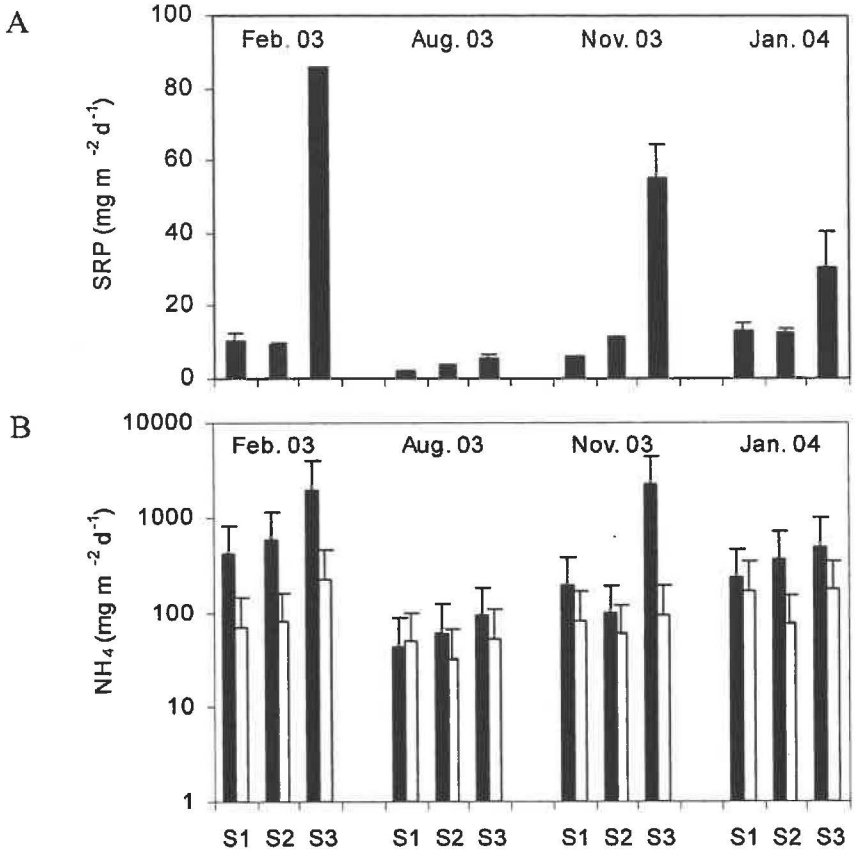

Figure 5.4: Mean fluxes of (A) soluble reactive phosphorus (SRP) and (B) ammonium (NH_4), for sites 1 (S1), 2 (S2) and 3 (S3) from four periods of light chamber deployment. Error bars represent standard errors. For NH_4, dark bars represent initial release rates (0-12 h) and light bars represent secondary release rates (12-48 h).

Table 5.4: Two-way analysis of variance between period, chamber type (light or dark) and period x chamber for fluxes of soluble reactive phosphorus (SRP) and ammonium in the phase 0 to 12 h (NH_4 1) and 12 to 48 h (NH_4 2) at site 1 and site 2. df is degrees of freedom, MS is mean squares, F is the test statistic and p is probability.

		Site 1				Site 2			
Fluxes	**Factor**	**df**	**MS**	**F**	**p**	**df**	**MS**	**F**	**p**
SRP	Period	3	93	1.88	0.211	3	152	18.58	< 0.01
	Chamber	1	7	0.14	0.722	1	44	5.36	0.05
	Period x Chamber	3	11	0.22	0.883	3	142	17.39	< 0.01
	Error	8	49			8	8		
NH_4 1	Period	3	88717	30.81	< 0.01	3	259983	56.58	< 0.01
	Chamber	1	4824	1.68	0.232	1	810886	176.48	< 0.01
	Period x Chamber	3	1464	0.51	0.687	3	240907	52.43	< 0.01
	Error	8	2880			8	4595		
NH_4 2	Period	3	22754	12.55	< 0.01	3	71205	9.93	< 0.01
	Chamber	1	7899	4.36	0.070	1	72473	10.11	0.01
	Period x Chamber	3	2410	1.33	0.331	3	60865	8.49	< 0.01
	Error	8	1813			8	7170		

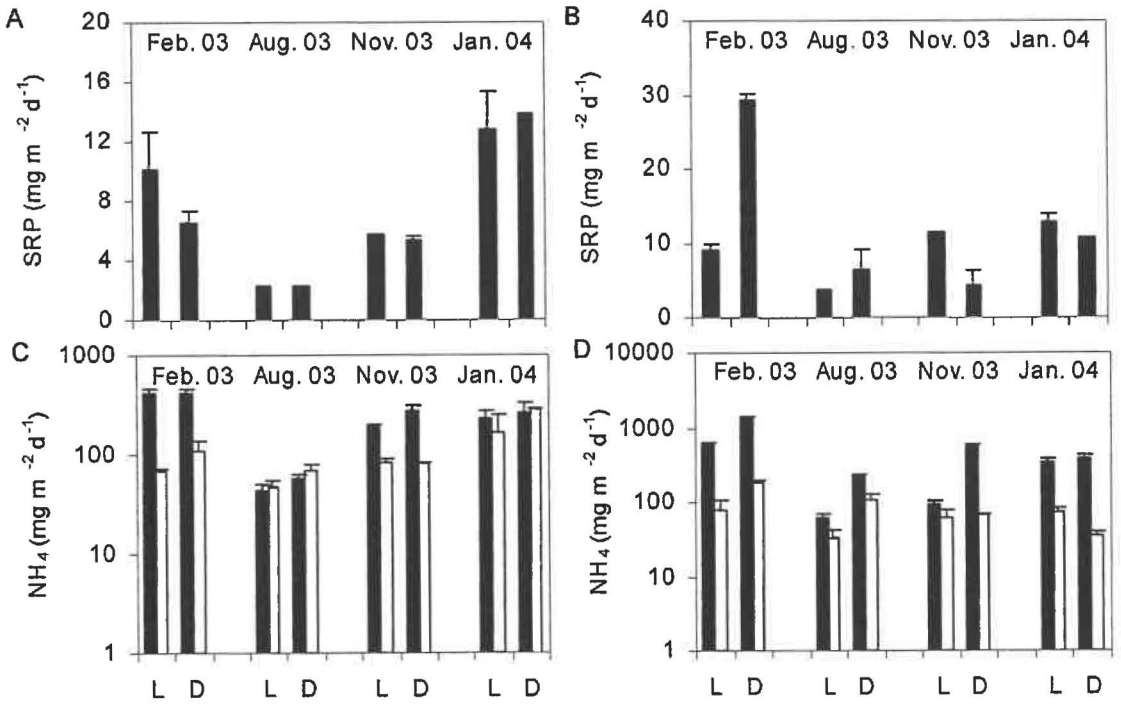

Figure 5.5: Fluxes of soluble reactive phosphorus (SRP) at (A) site 1 and (B) site 2, and fluxes of ammonium at (C) site 1 and (D) site 2 for light (L) and dark (D) benthic chambers for four periods of chamber deployment. Error bars represent standard errors. For NH_4, dark bars represent initial release rates (0-12 h) and light bars represent secondary release rates (12-48 h).

5.4 Discussion

5.4.1 Sediment nutrient fluxes

Release rates of SRP of up to 86 mg m^{-2} d^{-1} estimated from this study are considerably higher than those of 7 to 50 mg m^{-2} d^{-1} observed in other eutrophic lakes (Nürnberg, 1988; Marsden, 1989), although rates between 100 and 200 mg P m^{-2} d^{-1} have been obtained from sediment cores incubated in the laboratory at high summer temperatures (Søndergaard, 1989; Jensen and Anderson, 1992). Previous summer estimates of P release in Lake Rotorua, based on changes in hypolimnion concentration during a stratification event, were within the range observed here (20-40 mg SRP m^{-2} d^{-1}, White et al., 1978).

Sediment release rates of SRP remained relatively invariant through time in all chambers, irrespective of initial DO concentration or changes in DO. While SRP release rates are generally reported to be much higher during water column anoxia than under well oxygenated conditions (Anderson and Ring, 1999; Nowlin et al., 2005), there is evidence in sediment core incubations for high release rates under aerobic water column conditions (Søndergaard 1989; Jensen and Anderson, 1992; Krivstov et al., 2001). It has been suggested that SRP release under aerobic conditions is associated with high rates of organic material decomposition at the sediment-water interface (Marsden, 1989; Kleeberg and Kozerski, 1997). Rapid decomposition utilises oxygen and nitrate and may create localised reducing conditions leading to desorption of P from metal cation complexes (Kleeberg and Kozerski, 1997; Krivtsov et al., 2001). Although the results of this study suggest that high release rates of P already occur in Lake Rotorua when the overlying water is aerobic, the possibility should not be discounted that there are even greater release rates when the overlying water is anoxic, in association with summer stratification events, such as the events described in Chapter 2.

Gächter et al. (1988) suggest that SRP release rates may also be partly controlled by changes in sediment microbial physiology, including uptake, storage and release of P, as well as production and decomposition of bacterial biomass. Rates of P sedimentation are high in Lake Rotorua (7 - 65 mg TP m^{-2} d^{-1}, see Chapter 4) and are therefore likely to be important in sustaining the high release rates observed in this

study, particularly at the deeper sites. The large seasonal differences in release rates observed may be explained in part by changes in temperature, which controls rates of biological activity, as well as oxygen consumption rates and redox potential (Boström and Pattersson, 1982; Søndergaard, 1989; Søndergaard 2003). Seasonal variability in sedimentation rates observed in the lake in Chapter 4 may also be important.

A two-phase release rate was observed in the chamber incubations for NH_4. A sustained high initial rate of release in the first 12 h of chamber deployment was followed by a lower secondary release rate over the remaining 12 to 48 h. Increases in dissolved inorganic nitrogen (DIN) concentration in sediment core incubations are typically found to be linear through time (Fukuhara and Sakamoto, 1988), although often only one measurement is collected following the first 24 h of incubation, which would not have captured the trends observed here. It is possible that our NH_4 fluxes may have been artificially enhanced by isolation of the sediments or disturbance of the porewaters during deployment, though there was no evidence of this phenomenon in association with SRP release. Further, the absence of NO_3 in the chambers suggests that nitrification did not occur or that if there was nitrification, the rate of denitrification was sufficiently rapid to remove NO_3.

The release rate of NH_4 may have been associated with a decrease in bacterial metabolism and regeneration of NH_4 as the water column becomes progressively deoxygenated during each deployment. For example, before deployment of the chambers, high ammonium regeneration rates may be coupled to rapid nitrification and denitrification at the sediment-water interface. As DO decreases inside the chambers immediately after deployment, nitrification may be shut down, leading to rapid build up of ammonium and lack of nitrate to support denitrification. Further, the secondary release rate observed in our chamber deployments may therefore represent the natural organic matter degradation rate normally observed under low DO. Without further experimental work involving artificial control of DO inside the chambers during incubations, it is difficult to ascertain the exact mechanisms leading to the high variability of ammonium release observed over time within chambers.

Release rates of NH_4 of up to 2212 mg m^{-2} d^{-1} estimated in this study are also much higher than those observed elsewhere. In a literature review of NH_4 release rates in

freshwater systems, Hargreaves (1998) lists a highest value of 185 mg m^{-2} d^{-1} while Fukuhara and Sakamoto (1988) found DIN release rates of between 0.7 and 240 mg m^{-2} d^{-1}. Previous sediment release estimates for Lake Rotorua of 250-530 mg NH_4 m^{-2} d^{-1} (White et al., 1978), based on changes in hypolimnion concentration during a stratification event, were within the range observed here. High rates of NH_4 release have been found to coincide with high organic matter sedimentation rates (Fukuhara and Sakamoto, 1988) and in Lake Rotorua, sedimentation rates of up to 228 mg TN m^{-2} d^{-1} have been observed, with rates increasing significantly with water column depth (Chapter 4).

The lack of a significant difference in sediment SRP and NH_4 release rates between light and dark benthic chambers at site 1 suggests that primary productivity at the sediment-water interface may not have an important influence in mediating nutrient fluxes in shallow regions, perhaps as a result of high rates of advective transport and sediment disturbance not allowing an opportunity for significant accumulation of periphyton biomass. By contrast, at intermediate depths where there are high rates of deposition of chlorophyll (Burger, 2005), there may still be sufficient light for production and respiration by benthic algae to influence nutrient uptake rates between light and dark chambers (cf. Dodds, 2003). For example, despite very low light levels at site 2 (< 1 % of surface irradiance), rates of SRP and NH_4 release, and SOD were all lower in light than in dark chambers.

5.4.2 Verification of rates

A 19-day stratification event commencing 1 February 2003 coincided with chamber deployments commencing 10 February 2003. Sediment release rates of SRP during the stratification event, calculated from increases in SRP concentrations below the thermocline, and after accounting for sedimentation, inflows and diffusion across the thermocline, were estimated to be 13.8 mg m^{-2} d^{-1} (Burger et al., 2005). For this study, a mean SRP release rate beneath the thermocline of 17.4 mg m^{-2} d^{-1} was calculated for the same period using an estimate of SRP release rate at each 1 m depth interval beneath the thermocline, derived from linear interpolations between light chamber measurements at the three sites. The similarity between SRP release rates derived from our chamber measurements and those estimated using changes in

hypolimnion concentration suggest that chamber measurements are indeed representative at the lake scale.

Hypolimnion NH_4 concentrations during the same stratification event in February 2003 increased from 0.046 to 0.291 mg L^{-1}, representing a mean release rate of 63.9 mg m^{-2} d^{-1} for bottom sediments below the thermocline. This rate is substantially lower than that estimated mean release rate beneath the thermocline from the chamber deployments for the same period (131.2 mg m^{-2} d^{-1}), which was derived from the second rate of NH_4 release (12 to 48 h) observed in the light chambers and calculated as for SRP. However, estimates from the chambers do not incorporate loss of NH_4 due to nitrification, as may occur higher in the water column, or uptake by benthic organisms.

5.4.3 Internal versus external loads

Fluxes of nutrients in Lake Rotorua, based on data presented in Table 5.5, indicate that bottom sediments are the dominant source of N and P (Fig. 5.6). Mean SRP and NH_4 sediment release rates at all sites, calculated from the current study, were at least three times greater than the mean daily external load determined in this thesis in Chapter 6 (Table 5.5). Mean release rates of SRP at site 3 exceeded mean TP sedimentation rates at the same site (Table 5.5), indicating the importance of the deeper sediments as a source of SRP to the water column. The fluxes did not include estimates of porewater SRP and NH_4 remobilisation in the shallow regions of the lake due to resuspension, or releases of dissolved organic phosphorus and dissolved organic nitrogen, that would have resulted in elevation of TP and TN releases above those measured for SRP and NH_4. Rates of water column denitrification, which may have important implications for the loss of N from the lake, were also not measured directly in the present study.

The high nutrient release rates observed in Lake Rotorua reflect the large pool of nutrients accumulated in the lake's sediments as a result of several decades of high rates of external loading, particularly in association with wastewater inputs to the lake. High nutrient release rates can be expected to continue in this lake, given the high organic matter sedimentation rates and anoxia of bottom sediments, and only a severe reduction in the external load may effectively 'break' the depositional cycle.

Table 5.5: Source and description of nutrient load components used in Fig.5.6.

Component	Reference	Period	Method
External nutrient load	Chapter 6	Jan. 01-Dec. 03	Daily loads associated with 9 major, 17 minor and ungauged inflows, and rainfall
Sedimentation rates	Chapter 6	Feb. 03-Jan. 04	Sediment trap deployments coinciding with chamber deployments in this study
Outflows	Beya et al., 2005	Jan. 02-Dec. 02	Monthly nutrient loads in single outflow

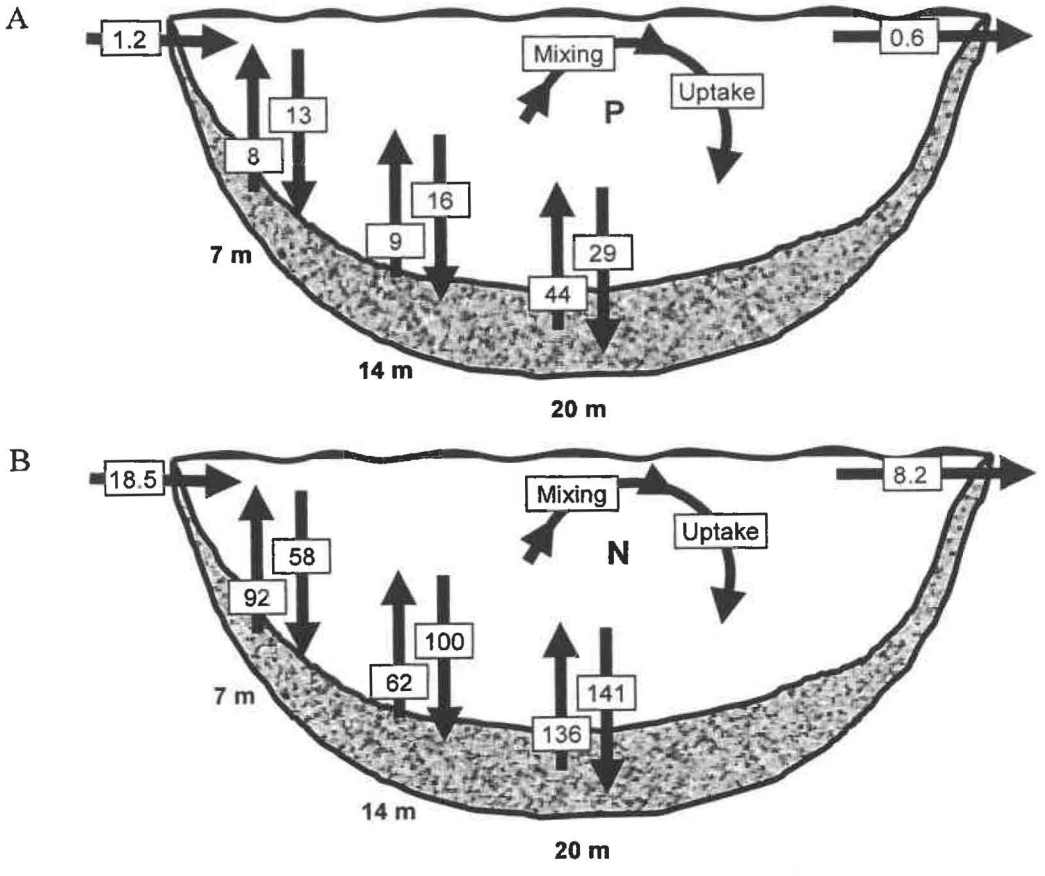

Figure 5.6: Cycling of (A) phosphorus and (B) nitrogen in Lake Rotorua. All units are expressed as aerial rates (mg m^{-2} d^{-1}). Inflow, outflow and sedimentation rates represent total concentrations (TP or TN) and sediment release rates represent soluble reactive phosphorus (SRP) or ammonium (NH_4, secondary release rate). Sedimentation and sediment release rates are expressed as a seasonal mean calculated over the four sampling periods. Inflow and outflow concentrations are derived from Chapter 6 and Beyá et al., (2004), respectively, and sedimentation rates are derived from Chapter 4. See Table 5.5 for sources of inflow, outflow and sedimentation rates.

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Chapter 6: Modelling the relative influence of external and internal nutrient loads on water column nutrient concentrations and phytoplankton biomass[1]

Abstract

Lake Rotorua is a large (area 80 km^2), shallow (mean depth 10.8 m), polymictic lake in central North Island, New Zealand. Blooms of cyanobacteria and occasional anoxia of bottom waters characterise water quality in the lake over summer (Dec.-Mar.). This study used a vertically resolved water quality model, DYRESM-CAEDYM, to assist with quantifying the relative contributions of internal and external nutrient inputs to the lake, and their relative importance for phytoplankton biomass, with particular emphasis on cyanobacteria. External nutrient loads were derived for 26 tributaries as well as for groundwater and stormwater flows. The total external load was 534 t yr^{-1} for total nitrogen and 34 t yr^{-1} for total phosphorus. Other forcing inputs to the model included meteorological data collected at a station beside the lake and discharge from the only outflow, Ohau Channel. Measured rates of sediment nutrient release obtained from benthic chamber measurements, profiles of water column nutrient concentrations, surface chlorophyll *a* concentration and continuous temperature and dissolved oxygen measurements were used to validate output from the DYRESM-CAEDYM model. Simulations of water column temperature and soluble reactive phosphorus (SRP) and ammonium (NH_4) concentrations matched field measurements closely, and captured the timing and duration of stratification events and subsequent changes in bottom water nutrient concentrations. Model simulations of different nutrient loading scenarios indicate that reductions in sediment nutrient fluxes would be more effective in reducing cyanobacterial biomass than similar reductions in catchment fluxes, due to the incidence of large sediment nutrient release events in association with summer blooms. This finding indicates that only a

[1] To be submitted to *Ecological Modelling* as: Burger, D.F., D.P. Hamilton and C. A. Pilditch: Modelling the relative influence of external and internal nutrient loads on water column nutrient concentrations and phytoplankton biomass in a eutrophic polymictic lake.

significant and prolonged reduction in external loads, that in turn reduces internal loads, will ultimately reduce cyanobacteria biomass in Lake Rotorua.

6.1 Introduction

Increased nutrient loads from anthropogenic sources have led to eutrophication of many aquatic systems worldwide (Wetzel, 1992). Attempts to reduce water column nutrient concentrations and mitigate phytoplankton blooms have generally focused on reductions of point sources from the catchment (Søndergaard et al., 2003). Even with severe constraints on point source loads to lakes, recovery from eutrophication has frequently been delayed due to high rates of internal recycling of nutrients between the sediments and overlying water column (Marsden, 1989; Søndergaard et al., 2003). In eutrophic lakes in particular, fluxes of nitrogen (N) and phosphorus (P) from the sediments to the water column often represent an important source of nutrients for primary productivity (Forsberg, 1989; Søndergaard et al., 1989).

Modelling assessments of lake eutrophication have often used mass balance equations (OECD, 1982), which provide a useful tool with which to then assess the response of phytoplankton biomass to changes in catchment P loads. However, these models do not capture the complex ecological phenomena that occur in natural systems, such as phytoplankton succession, potential for nutrient co-limitation or temporal evolution of recovery (Arhonditsis and Brett, 2005a). Coupled hydrodynamic-ecological models are therefore often used to capture these phenomena and to link transport processes with bio-geochemical cycles (Campos et al., 2001; Chan et al., 2002; Chen et al., 2002; Romero et al, 2004; Arhonditsis and Brett, 2005a). Many of the applications of these models have involved both gross simplifications of nutrient cycling and regeneration associated with bottom sediments, as well as limited validation of sediment nutrient release parameters. Sediment nutrient release rates have been found to be highly sensitive in model simulations (e.g. Schladow and Hamilton, 1995), leading to both overestimates and underestimates of water column nutrient concentrations (e.g. Romero et al., 2004; Arthonditsis and Brett, 2005b).

The use of acquired measurements and understanding of sediment nutrient fluxes in a coupled hydrodynamic-ecological model provides an opportunity to evaluate the

relative contributions of external and internal nutrient loads in a lake ecosystem. In polymictic lakes in particular, which have a sporadic regime of mixing and stratification, there may be tight coupling between the bottom sediments and water column, and strong seasonal and inter-annual variability in nutrient availability and phytoplankton phenology. While many of these processes can be examined individually (e.g. Burger et al., 2005; Chapter 5), the use of an inter-disciplinary model to capture this complexity may provide important insights to the eutrophication and management of polymictic eutrophic lakes.

Lake Rotorua, a eutrophic polymictic lake in the North Island New Zealand, has shown little change in lake trophic status despite removal of treated wastewater inputs from the lake in 1991 (Rutherford et al., 1996). The removal of wastewater inputs has had a minimal impact on water column nutrient and chlorophyll *a* (chl-*a*) concentrations and large blooms of potentially toxic cyanobacteria have continued to occur during summer. Total loads of soluble reactive phosphorus (SRP) and ammonium (NH_4) from the bottom sediments are comparable to external loads, but also show considerable variability depending on the frequency and duration of stratification events (see Chapter 5).

We hypothesise that internal nutrient loads, derived from sediment nutrient release, may be at least as important as external nutrient loads in the dynamics of phytoplankton biomass and succession in Lake Rotorua. The primary objective of this research was to apply a coupled hydrodynamic-ecological model to simulate current external and internal loading rates, and use model simulations to examine management scenarios of external versus internal load reductions on lake water column nutrient concentrations and cyanobacteria densities. A secondary objective of the study was to accurately determine annual external nutrient loads to the lake, in order to provide a better assessment of nutrient inputs to support management decisions for external nutrient load reduction strategies.

6.1.1 Study Site

Lake Rotorua is a large (area 79.8 km^2), shallow (mean depth 10.8 m) lake of volcanic origin in central North Island, New Zealand (Fig. 6.1). The lake catchment has an area of 425 km^2 which is dominated by agriculture (48 %) and plantation

forestry (23 %). There are nine major inflows (mean flow rate 0.22-2.75 $m^3 s^{-1}$), nine minor coldwater streams and eight minor geothermal streams (flow < 0.22 $m^3 s^{-1}$) (Table 6.1). Lake Rotorua has a water residence time of 540 days based on discharge from the only surface outflow, Ohau Channel. The lake is eutrophic (Rutherford et al., 1996), with annual mean concentrations of total phosphorus (TP) and total nitrogen (TN) of 0.055 mg L^{-1} and 0.814 mg L^{-1}, respectively (Burger et al., 2005). The phytoplankton community of the lake is dominated by cyanobacteria, *Anabaena* spp. and *Microcystis* spp., and exhibits co-limitation of N and P (see Chapter 3).

Until 1991, Lake Rotorua received wastewater from Rotorua city (population 60,000), which contributed annual loads of c. 35 tons P yr^{-1} and 150 tons N yr^{-1} (White et al., 1992). The lake stratifies for up to four weeks in summer, and stratification events are associated with rapid reductions in bottom water concentrations of dissolved oxygen (DO) and increases in NH_4 and SRP (Burger et al., 2005). Sediment nutrient fluxes, based on benthic chamber measurements, are as high as 85 mg SRP $m^{-2} d^{-1}$ and 2,200 mg NH_4 $m^{-2} d^{-1}$ (Chapter 5) and fluxes of SRP do not appear to be enhanced significantly by depletion of DO concentrations in water overlying the sediments. The high rates of organic matter deposition from the water column to the bottom sediments that have been described in Chapter 4 may be important in sustaining continuously high rates of sediment nutrient release.

6.2 Methods

6.2.1 Model description

DYRESM is a one-dimensional model which resolves vertical distributions of temperature, salinity and density in lakes and reservoirs based on a dynamic Lagrangian layer structure, which simulates the lake as horizontally uniform layers that expand and contract in response to heat, mass and momentum exchanges (see Imberger and Patterson, 1981; Gal et al., 2003). DYRESM has been coupled to the ecological model CAEDYM, which simulates up to seven phytoplankton groups (from taxa to species), DO, and several species of organic and inorganic nitrogen, phosphorus and carbon, using a series of partial differential equations that are characterised by rate constants (Robson and Hamilton, 2004).

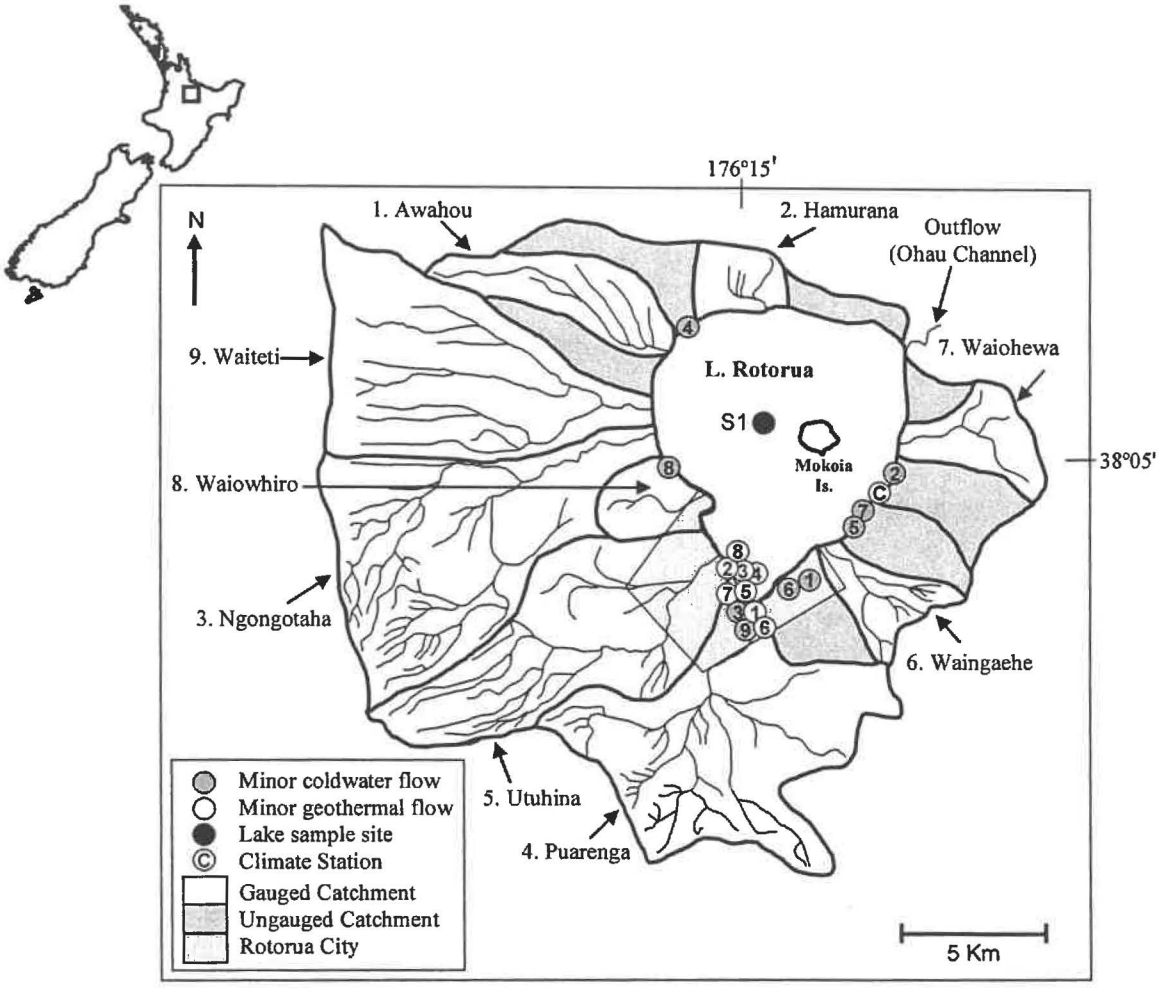

Figure 6.1: Map of Lake Rotorua and the nine dominant inflows and sub-catchments, nine minor coldwater inflows, eight minor geothermal inflows, lake sampling site (S1), Rotorua airport climate station and Rotorua City. Inflow numbers relate to Table 6.1.

These rate constants are defined by the user and vary in the model in response to other environmental variables (e.g. temperature, DO etc.). The bottom sediments are included in the model as a permanent sink for particulate matter that settles out of the water column, with releases of dissolved nutrients from the sediments prescribed from overlying water column properties (e.g. temperature, DO, pH). A concise documentation of CAEDYM and applications of it to lake and estuarine systems are given in Romero et al. (2004) and Robson and Hamilton (2004), respectively. In the present study the coupled DYRESM-CAEDYM model was run on an hourly time-step between 1 July 2001 and 31 March 2004, with daily input data for 12 inflows, meteorology and one outflow, and a daily output corresponding to midday. Due to the volcanic origin of the lake, a geothermal heat flux of 12 MW was supplied to the

bottom waters of Lake Rotorua to enhance vertical convective circulation in the bottom waters, allowing better representation of water column temperatures, particularly during stratification events. The application of a geothermal heat flux has also been used to model the hydrodynamics of other New Zealand volcanic lakes (e.g., Spigel et al., 2001).

6.2.2 Meteorological data

Daily meteorological data required as input to the DYRESM-CAEDYM model were taken from Rotorua Airport climate station adjacent to the lake (Fig. 6.1). Data included total daily rainfall and daily averages of hourly measurements of air temperature (°C), wind speed, short wave radiation, and hourly cloud cover, which was used to derive longwave radiation inputs (Fig. 6.2). Daily averages of hourly wet and dry bulb temperature and atmospheric pressure were used to derive mean daily water vapour pressure (Antenucci and Imerito, 2002) (Fig. 6.2).

6.2.3 Inflow and outflow data

The nine major inflows were assigned as independent inputs into the model. Continuous flow data for daily input to the model were available for only one major inflow, Ngongotaha Stream, during the study period of July 2001 to March 2004. Several years of historical flow data were available, however, for the Utuhina Stream (Jan.1991 to Apr. 1997), and Waingaehe, Waiohewa and Waiowhiro streams (Jul. 1992 to Jun. 1995). In addition, all major inflows were gauged monthly between July 1992 and March 2004. To estimate flows where data were not available, linear correlations were carried out between the Ngongotaha Stream discharge and that from each of the other major inflows except the Hamurana Stream, using all available data between 1991 and 2004 (mean R^2 = 0.6). The Hamurana Stream, a large, predominantly spring-fed inflow, was assigned a daily flow based on linear interpolation between monthly measurements for the period Jul. 2001 to Jun. 2004.

The eight geothermal inputs and nine minor streams were represented as two individual inflows in the model, as they contributed only 0.3 and 1.2 %, respectively, of total lake inflows (Table 6.1). Measured data for these inflows were restricted to monthly values collected between July 1992 and October 1994. Accordingly, daily flows over the current study period were estimated as a fixed proportion of the total

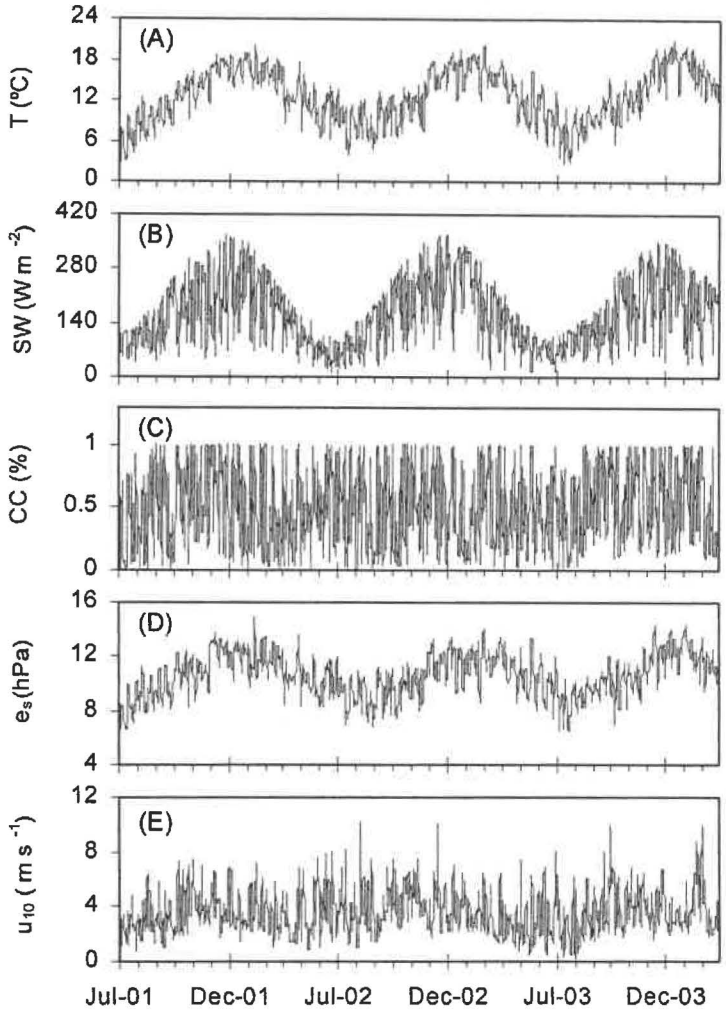

Figure 6.2: Meteorological data used as input to the DYRESM model, including (A) air temperature (T), (B) short wave radiation (SW), (C) cloud cover (CC), (D) vapour pressure (e_S) and (E) wind speed at a reference height of 10 m above the lake (u_{10}). All data were collected at the Rotorua Airport Climate station and represent daily means calculated from hourly measurements.

of all major inflows. Ungauged flows were estimated as the unknown term in a daily water balance equation that included the major and minor inflows, change in lake water storage based on hypsography and 7-day mean water level, to reduce short-term fluctuations from strong winds, rainfall, outflow from Ohau Channel and evaporation. Water level records were taken from Mission Bay on the north-eastern side of the lake, with interruptions in the data, typically only a few days, filled by linear interpolation. Mean daily discharge through the Ohau Channel (Fig. 6.1) was derived from a continuous water level recorder on the outflow and stage height-flow relationships. Water loss due to evaporation was calculated from the daily average evaporative heat flux (Fischer et al., 1979) using wind speed from Rotorua Airport

climate station and daily mean water temperatures from a temperature logger (ODYSSEY, Dataflow Systems Ltd) at 0.5 m depth at a central lake station (site 1, Fig. 6.1).

Table 6.1: Mean discharge and total annual nutrient loads of soluble reactive phosphorus (SRP), total phosphorus (TP), ammonium (NH_4), nitrate (NO_3) and total nitrogen (TN), for nine major inflows, nine minor coldwater inflows, eight minor geothermal inflows, ungauged inflows and rainfall, to Lake Rotorua. Means are based on the period Jan. 2002 to Jul. 2004. Flow number refers to the inflow location in Figure 6.1.

Inflow/Outflow	Name	Flow No.	Flow ($m^3 s^{-1}$)	SRP ($t yr^{-1}$)	TP ($t yr^{-1}$)	NH_4 ($t yr^{-1}$)	NO_3 ($t yr^{-1}$)	TN ($t yr^{-1}$)
Major inflows	Awahou Stream	1	1.62	3.48	3.95	0.45	58.80	62.16
	Hamurana Stream	2	2.75	7.54	8.29	1.03	60.04	66.45
	Ngongotaha Stream	3	1.42	1.58	2.21	0.60	34.32	48.18
	Puarenga Stream	4	1.52	2.44	3.14	3.21	48.89	62.33
	Utuhina Stream	5	1.59	2.74	3.25	2.13	36.68	47.59
	Waingaehe Stream	6	0.224	0.67	0.77	0.06	9.03	9.72
	Waiohewa Stream	7	0.283	0.29	0.52	13.21	12.20	24.73
	Waiowhiro Stream	8	0.301	0.41	0.47	0.21	8.40	9.66
	Waiteti Stream	9	1.072	1.45	2.15	0.83	41.04	45.44
	Sub Total		**10.79**	**20.59**	**24.76**	**21.74**	**309.40**	**376.27**
Minor cold-water inflows	Basley Road Stream	1	0.009	0.012	0.018	0.005	0.738	0.785
	Cookson's Wash	2	0.001	0.003	0.015	0.002	0.002	0.074
	Fenton Street Drain	3	0.000	0.000	0.000	0.000	0.001	0.003
	Hauraki Stream	4	0.005	0.001	0.008	0.008	0.051	0.104
	Lee Rd Tributary	5	0.021	0.013	0.058	0.033	1.223	1.491
	Lynmore Stream	6	0.053	0.072	0.146	0.042	5.425	5.850
	Swamp Rd Stream	7	0.031	0.025	0.056	0.032	2.577	2.834
	Te Ahipukahu Tributary	8	0.062	0.055	0.085	0.023	1.858	2.233
	Te Ngae Road Drain	9	0.026	0.185	0.270	0.326	0.029	0.706
	Sub Total		**0.208**	**0.366**	**0.655**	**0.472**	**11.903**	**14.079**
Minor geothermal inflows	Black Stream	1	0.006	0.048	0.064	0.187	0.005	0.352
	Ohinemutu Springs	2	0.010	0.024	0.031	0.083	0.004	0.152
	Pipe Stream	3	0.003	0.006	0.020	0.025	0.000	0.055
	Polynesian North	4	0.011	0.069	0.097	0.375	0.001	0.479
	Polynesian South	5	0.001	0.009	0.014	0.013	0.000	0.019
	Sewer Stream	6	0.014	0.131	0.143	0.040	0.001	0.114
	Springs Outlet	7	0.002	0.015	0.018	0.037	0.002	0.073
	Tunuhopu Springs	8	0.007	0.014	0.044	0.019	0.032	0.147
	Sub Total		**0.054**	**0.316**	**0.432**	**0.778**	**0.046**	**1.392**
Other	Total Ungauged		3.17	6.05	7.35	6.54	91.36	111.37
	Rainfall		2.66	1.34	1.34		29.24	29.24
	Sub Total		**5.83**	**6.05**	**8.69**	**6.54**	**120.60**	**140.61**
Total	**Inflows**		**16.88**	**27.32**	**34.53**	**29.53**	**441.94**	**532.36**

6.2.4 Inflow water quality

Water quality variables for each of the model inflows included daily estimates of water temperature (°C), DO, SRP, TP, NH_4, nitrate (NO_3) and TN concentrations (mg L^{-1}), and pH. For the major inflows, values were estimated from linear interpolations between monthly measurements collected over the study period (Environment Bay of Plenty, unpubl. data). Due to the dominance of spring-fed inflows to the lake, the use of the rating-curve method (e.g. Crawford, 1991) to derive inflow nutrient loads from linear correlations between flow rate and nutrient concentration was not applied.

Missing monthly measurements were replaced by monthly mean values calculated over the whole study period. For all streams except Awahou, water temperatures were estimated from daily mean air temperature based on correlations ($R^2 > 0.71$) between Rotorua airport temperature and monthly stream temperature. For Awahou Stream, where water temperature was less closely correlated with air temperature ($R^2 = 0.38$) and annual variability in water temperatures was < 2 °C, linear interpolations between monthly measurements were used. For all major inflows, DO concentrations were assumed to be at saturation and were estimated from the assigned daily water temperature (Hamilton and Schladow, 1997).

For the minor coldwater and geothermal inflows, measurements of water temperature, DO and nutrient concentrations (TP, SRP, TN, NH_4 and NO_3), and pH were available only for the period July 1992 to October 1994 (Environment Bay of Plenty, unpubl. data). Based on these data, minor coldwater inflows had similar composition to the major inflows, and each variable was therefore approximated as a volumetric mean value for major inflows on each day of the modelling period. Daily values for each water quality variable for the residual inflow were also estimated by this method. Geothermal inflows had very different characteristics to coldwater inflows, with volumetric means showing high temperature (34.9 °C), high nutrient concentrations, particularly SRP and NH_4 (0.187 and 0.479 mg L^{-1}, respectively) and low DO concentration (2.4 mg L^{-1}). A constant value for each day was applied for each variable in the geothermal inflows, calculated as the volumetric mean of all eight geothermal inflows for the period July 1992 to October 1994.

Table 6.2: Phytoplankton parameter values used in CAEDYM. Cyano represents cyanobacteria and other represents a combined diatoms and chlorophyte assemblage.

Phytoplankton parameters	Symbol	Units	Cyano	Other	References/remarks
Maximum potential growth rate at 20°C	$\mu_{max\,i}$	day^{-1}	0.7	1.8	Robson & Hamilton, 2004
Irradiance parameter non-photoinhibited growth	I_{ki}	$\mu Em^{-2}s^{-1}$	120	20	Robson & Hamilton, 2004
Photoinhibited saturation irradiance	I_S	$\mu Em^{-2}s^{-1}$	200	10	Wallace and Hamilton, 1999
Half-saturation constant for phosphorus uptake	K_{Pi}	$mg\ L^{-1}$	0.006	0.01	Holm & Armstrong, 1981
Half-saturation constant for nitrogen uptake	K_{Ni}	$mg\ L^{-1}$	0.03	0.045	Hamilton & Schadow, 1997
Minimum internal nitrogen concentration	$IN_{min\,i}$	mg N (mg chl *a*)$^{-1}$	2.5	2	Robson & Hamilton, 2004
Maximum internal nitrogen concentration	$IN_{max\,i}$	mg N (mg chl *a*)$^{-1}$	4	5	Robson & Hamilton, 2004
Maximum rate of nitrogen uptake	$UN_{max\,i}$	mg N (mg chl *a*)$^{-1}$ d^{-1}	1.5	3	Robson & Hamilton, 2004
Minimum internal phosphorus concentration	$IP_{min\,i}$	mg P (mg chl *a*)$^{-1}$	0.5	0.25	Robson & Hamilton, 2004
Maximum internal phosphorus concentration	$IP_{max\,i}$	mg P (mg chl *a*)$^{-1}$	2.2	2	Hamilton & Schadow, 1997
Maximum rate of phosphorus uptake	$UP_{max\,i}$	mg P (mg chl *a*)$^{-1}$ d^{-1}	0.3	1	Hamilton & Schadow, 1998
Temperature multiplier for growth limitation	Ψ_i	dimensionless	1.08	1.06	Robson & Hamilton, 2004
Standard temperature for growth	$T_{sta\,i}$	°C	20	12	Griffin et al., 2001
Optimum temperature for growth	$T_{opt\,i}$	°C	28	23	Griffin et al., 2002
Maximum temperature for growth	$T_{max\,i}$	°C	35	30	Griffin et al., 2003
Respiration rate coefficient	k_{Ri}	per day	0.05	0.12	Robson & Hamilton, 2004
Temperature multiplier for respiration	Vr	dimensionless	1.09	1.05	Robson & Hamilton, 2004
Constant settling velocity	$W_{S\,i}$	$m\ s^{-1}$	0.5×10^{-5}	-0.06×10^{-5}	Romero et al., 2004

6.2.5 Phytoplankton

The dynamics of two phytoplankton groups, represented by equivalent chl-*a* concentration, were simulated in the model; buoyant species representing cyanobacteria and non-buoyant species considered to be represented by other major taxa, mostly chlorophytes and diatoms (see Chapter 3). Phytoplankton parameters for these groups were assigned based on literature values (e.g. Holm and Armstrong, 1981: Grover et al., 1999; Wallace and Hamilton, 1999; Robson and Hamilton, 2004) or were calibrated within ranges given by literature values (Table 6.2). Initial lake water column concentrations of chl-*a* for the two phytoplankton groups were proportioned according to cell counts (Chapter 3). The effects of zooplankton grazing on phytoplankton were not simulated explicitly, however, their contribution to phytoplankton mortality was included in the model through a general phytoplankton loss term.

6.2.6 Sediment parameters

Sediment SRP and NH_4 release rates and sediment oxygen demand inputs to CAEDYM were based on benthic chamber experimental measurements conducted in Lake Rotorua within the period of modelling (Chapter 5). The measurements included quantification of inorganic sediment nutrient release rates for four periods at three sites between February 2003 and January 2004. The release rates of SRP and NH_4

obtained using the chambers were found to cover a range of values that included estimates of sediment nutrient release based on changes in hypolimnion SRP and NH_4 concentration during a stratification event (Chapters 2 & 5).

6.2.7 Model Validation

The model was calibrated against field data over a one-year period (commencing 1 Jul. 2001) using comparisons of temperature and DO, nutrient (TP, SRP, TN, NH_4 and NO_3) and chl-*a* concentrations. The final two years of the study period (commencing 1 Jul. 2002) were used to validate the calibrated model. Field data were obtained from a variety of sources. Daily average water temperature profiles were derived from measurements taken at 5 min intervals from thermistors (ODYSSEY Ltd) deployed at 2 m depth intervals at a central lake station (site 1, Fig. 6.1) between November 2002 and March 2004. Daily average bottom (depth 19 m) DO concentrations for the period February 2003 to March 2004 were taken with an *in situ* dissolved oxygen logger (Greenspan Technology Ltd) at 30 min intervals. Conductivity-temperature-depth (CTD) profiles (Seabird Electronics) taken approximately monthly at site 1 (Fig. 6.1) between July 2001 and March 2004 provided vertical distributions of temperature, DO and photosynthetically available radiation (PAR, Licor Ltd.) (Gibbons-Davies, 2003; Scholes, 2004a, 2004b). Concentrations of chl-*a*, NH_4, NO_3, SRP, TP and TN were analysed from samples collected from a depth-integrated sample of the surface-mixed layer (0-8 m) and from discrete bottom water (0.5-1.5 m above lake-bed) samples, collected concurrently with monthly CTD profiles. Field data on dissolved and particulate organic nutrient concentrations were not available over the current study period to validate model output on labile and refractory particulate organic N and P.

6.2.8 External load

The external nutrient load of SRP, TP, NH_4, NO_3 and TN to Lake Rotorua was estimated for the period 1 January 2002 to 31 December 2003 as the product of mean nutrient concentrations and mean flow rate for each of the 26 individual inflows (Table 6.1). Mean nutrient concentrations for the nine major flows were taken from monthly measurements over this period, and from measurements for the period July 1992 to October 1994 for the minor coldwater and geothermal inflows. Nutrient loads associated with the residual inflow were estimated as the product of the volume and

the volumetric mean concentration calculated over all measured inflows. Atmospheric deposition of nutrients was estimated as the product of an annual aerial deposition rate of 0.17 kg TP ha^{-1} yr^{-1} (Schouten, 1983) and 3.7 kg TN ha^{-1} y^{-1} (Elliot and Stroud, 2001), and lake surface area (79.8 km^2).

6.2.9 Management Scenarios

Two scenarios of nutrient loading were examined in model simulations. In the first scenario, external loads of TN were reduced by 47 % to equate to a 250 t yr^{-1} reduction of TN, based on targets set for Lake Rotorua (see Rutherford et al., 1989). The aim of the proposed target reductions was to restore lake water quality to levels similar to the 1960s, before persistent summer phytoplankton blooms were first observed in the lake. External TP loads were also reduced by 47 % in the first management scenario. The second scenario involved a reduction of internal nutrient loads by 47 %, to allow direct comparison with the external load reduction scenario.

6.3 Results

6.3.1 Catchment flow analysis

The nine major inflows collectively represent 64 % of all inflows to Lake Rotorua and have a mean discharge of 10.8 m^3 s^{-1} (Table 6.1). Total discharge from these inflows was up to 37.8 m^3 s^{-1} during storms, while minimum flows never declined below 9.3 m^3 s^{-1} (Fig. 6.3). The Hamurana Stream is the largest of the nine major inflows and has a mean discharge of 2.8 m^3 s^{-1}, nearly 1.2 m^3 s^{-1} higher than the second largest inflow, Awahou Stream. The mean total discharge of the nine minor coldwater inflows is 0.21 m^3 s^{-1} (Table 6.1). Discharge from the eight minor geothermal inflows is approximately 0.05 m^3 s^{-1} or 0.3 % of the total discharge to the lake, and ungauged inflows represent c. 19 % of the total discharge to the lake (mean 3.2 m^3 s^{-1}). Discharge from ungauged inflows is slightly higher than that from rainfall (mean 2.7 m^3 s^{-1}) and that from the sum of all 18 coldwater and geothermal inflows (Fig. 6.3). Mean discharge through the Ohau Channel outflow is 15.3 m^3 s^{-1}, with a high degree of variability through the study period (range 9.5-27.0 m^3 s^{-1}) (Fig. 6.3). Evaporation accounted for 2.1 m^3 s^{-1} of water lost from the lake and was as high as 7 m^3 s^{-1} in summer (Fig. 6.3).

6.3.2 External nutrient load

Total external TP and TN loads to Lake Rotorua from all inflows are 35 and 532 t yr^{-1}, respectively (Table 6.1). Greater than 70 % of the total nutrient load is contributed by the nine major inflows (24.8 t TP yr^{-1} and 376.3 t TN yr^{-1}), 21 % by ungauged inflows (7.4 t TP yr^{-1} and 111.4 t TN yr^{-1}) and between 4 and 6 % by direct rainfall on the lake (1.3 t TP yr^{-1} and 29.2 t TN yr^{-1}). Minor inflows constitute less than 3 % of the total nutrient load to the lake.

Of the nine major inflows, the Hamurana Stream is the dominant source of TP to the lake, representing nearly 34 % of the total load (Table 6.1). The Awahou, Utuhina and Puarenga Streams are also important sources of phosphorus, each contributing between 13 and 16 % of the total P load, while the three smallest major inflows (Waingaehe, Waiohewa and Waiowhiro) each contribute less than 4 % of the total load. Phosphorus loads are predominantly in the form of SRP, constituting 83 % of TP load. Nitrogen loads are more evenly distributed amongst the major inflows, with six streams each contributing between 12 and 18 % of the total load (Awahou, Hamurana, Ngongotaha, Puarenga, Utuhina and Waiteti Streams). The Hamurana Stream contributes the largest N load to the lake (66 t TN yr^{-1}). Nitrogen loads are predominantly in the form of NO_3 (82 % of mean TN load), except for the Waiohewa Stream, for which NH_4 represents 54 % of TN loads due to the association of this discharge with geothermal sources.

The nine minor coldwater flows collectively contribute 0.7 tonnes of TP and 14 tonnes of TN to the lake annually. As for the major inflows, NO_3 constitutes 85 % of TN though only 56 % of TP is in the form of SRP. The eight minor geothermal inflows contribute 0.4 t TP yr^{-1} and 1.4 t TN yr^{-1}. Ammonium constitutes 60 % of the TN load from geothermal sources. Rainfall contributes 1.3 t TP yr^{-1} and 29.2 t TN yr^{-1} (Table 6.1). The nutrient load associated with ungauged inflows is estimated to be 7.4 t TP yr^{-1} and 111.4 t TN yr^{-1}, representing c. 21 % of the total nutrient load to the lake (Table 6.1).

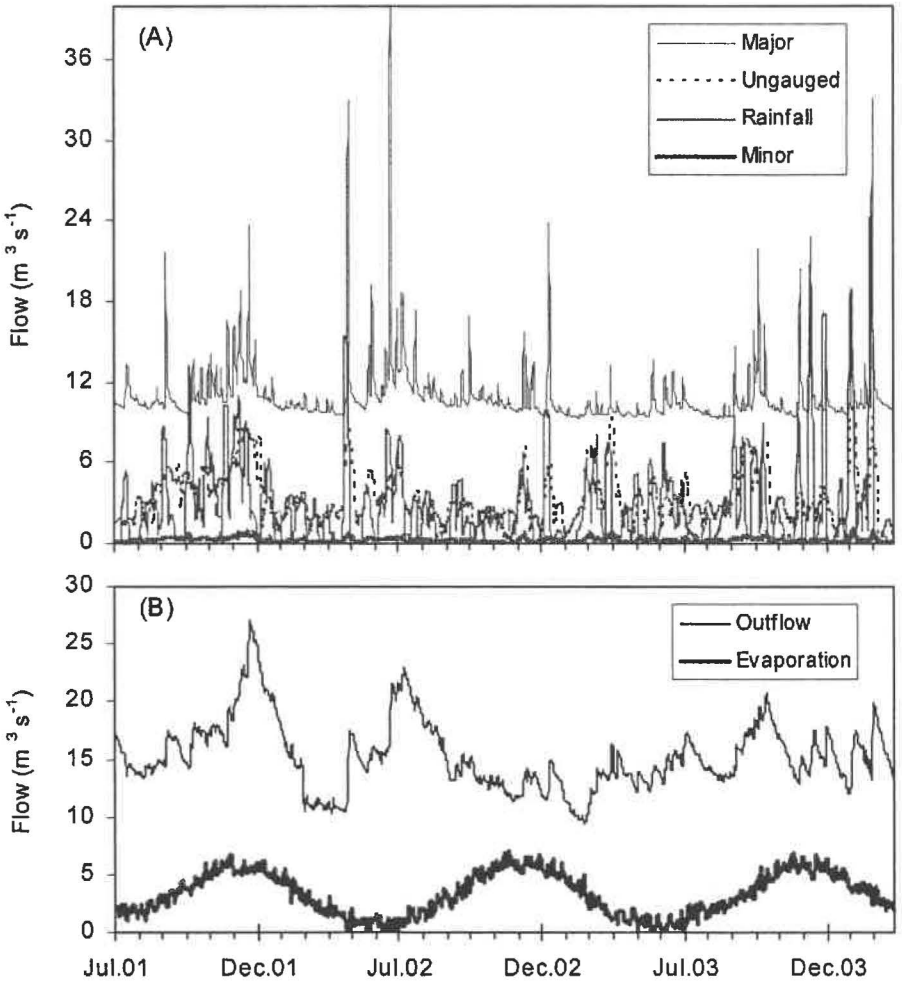

Figure 6.3: Mean daily (A) inflows and (B) outflows for Lake Rotorua, Jul. 2001 to Apr. 2004. For (A), major represents the nine major inflows, ungauged is unmeasured inflows due to groundwater, ungauged catchment and storm water runoff and minor represents all 17 minor geothermal and coldwater inflows (see Table 6.1). For (B), outflow represents discharges from the Ohau Channel.

6.3.3 Model simulations

Model simulations of lake water levels are similar to observed values (Fig. 6.4), with minor differences due to variations between estimates of evaporation for the water balance and the model simulations, with the latter based on simulated surface water temperature rather than actual measurements. Simulations of water column temperature agreed well with measured temperature using the model parameters set out in Table 6.3 ($R > 0.9$, Table 6.3). Variations between simulated and observed values were generally less than 1.5 °C through the water column (Fig. 6.5). The

timing and duration of stratification events were captured accurately over the two summer periods for which field thermistor data were available (Fig. 6.5), although simulations slightly underestimated the depth of the thermocline in January 2004. Over the whole period (Jun. 2001 - Apr. 2004), simulations of temperature (± SD) at 1.5 m (hereafter referred to as surface water) were 0.74 ± 0.63 °C lower than corresponding observed values (Fig. 6.6), with differences greater in winter (Jun.-Sep., -1.03 ± 0.38 °C) than in summer (Dec-Mar, -0.42 ± 0.81 °C). Mean simulated temperature at depth 19 m (hereafter referred to as bottom waters) was 0.36 ± 0.78 °C lower than observed values over the same period (Fig. 6.6), with differences also higher in summer (-0.61 ± 0.58 and -0.05 ± 1.02 °C, respectively).

Table 6.3: Statistical comparison between model simulations and monthly field measurements of surface (depth integrated, 0-8 m) and bottom (depth 19 m) temperature and concentrations of dissolved oxygen (DO), soluble reactive phosphorus (SRP), total phosphorus (TP), ammonium (NH_4), nitrate (NO_3), total nitrogen (TN) and chlorophyll *a* (Chl-*a*), over the calibration (Cal., Jul. 2001-Jun. 2002) and validation (Val., Jul. 2002-Apr. 2004) period. RMSE represents root mean square error. Chl-*a* concentrations in bottom waters were not examined.

	Surface mixed layer				Bottom waters			
	RMSE		R		RMSE		R	
	Cal.	Val.	Cal.	Val.	Cal.	Val.	Cal.	Val.
Temperature (°C)	0.984	0.940	0.99	0.99	1.018	0.733	0.99	0.99
DO (mg L^{-1})	0.906	1.366	0.92	0.63	1.301	1.492	0.86	0.93
SRP (mg L^{-1})	0.009	0.007	0.38	0.16	0.013	0.013	0.61	0.91
TP (mg L^{-1})	0.012	0.013	0.80	0.40	0.013	0.022	0.72	0.76
NH_4 (mg L^{-1})	0.022	0.030	0.42	-0.02	0.032	0.106	0.75	0.96
NO_3 (mg L^{-1})	0.005	0.021	-0.36	0.02	0.029	0.009	-0.33	0.75
TN (mg L^{-1})	0.117	0.213	0.24	0.41	0.145	0.284	0.27	0.63
Chl-*a* (ug L^{-1})	8.424	11.900	0.37	0.12				

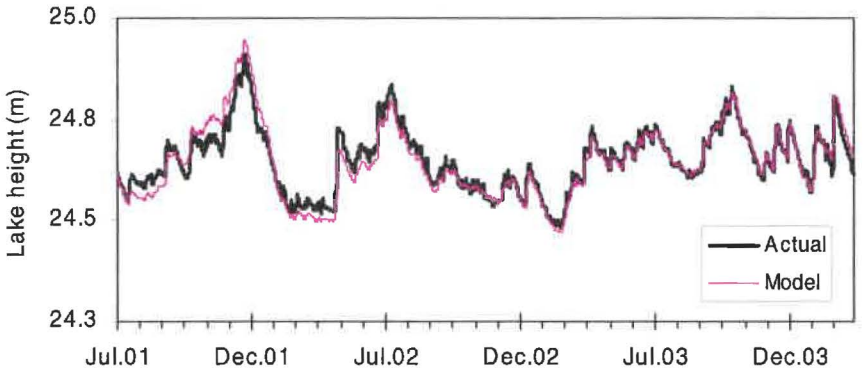

Figure 6.4: Mean daily values of lake water column height during the model period (Jul. 2001-Apr. 2004), as measured by the Mission Bay recorder station (Actual) and simulated by the DYRESM model (Model).

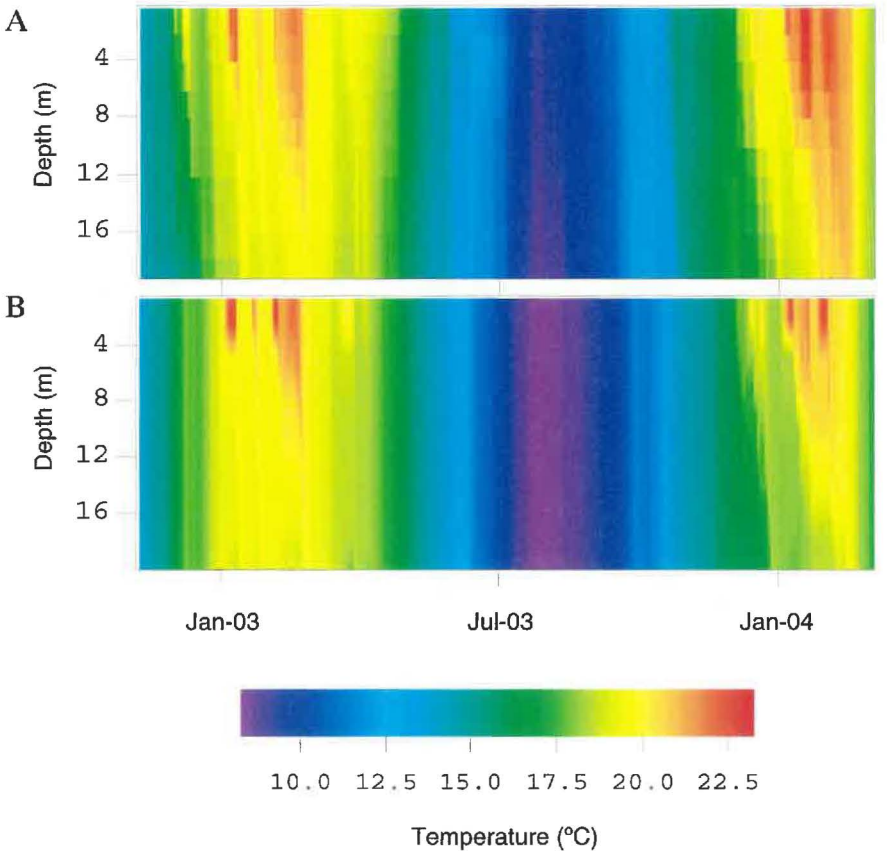

Figure 6.5: Temperatures (°C) in Lake Rotorua derived from (A) daily means of temperature loggers deployed at 2 m depth intervals, and (B) daily output from model simulations, for the period Nov. 2002-Apr. 2004.

Table 6.4: Physical data inputs and parameters for DYRESM model.

Coefficient/variable	Value	Unit	Reference
Benthic boundary layer thickness	0.1	m	
Bulk aerodynamic momentum transport coefficient	0.0013		Stull (1988)
Critical wind speed	4	$m\ s^{-1}$	
Emissivity of water surface	0.96		Imberger and Patterson (1981)
Lake latitude	-38	°N	
Light extinction coefficient (K_d)	0.8	m^{-1}	Field
Mean albedo of water	0.07		Patten et al. (1975)
Min/max layer thickness	1.0/4.0	m	
Potential energy mixing efficiency	0.25		Spigel et al. (1986)
Shear production efficiency	0.08		Spigel et al. (1986)
Vertical mixing coefficient	400		
Wind stirring efficiency	0.6		Imberger (1998)
Geothermal heat flux	12	mW	

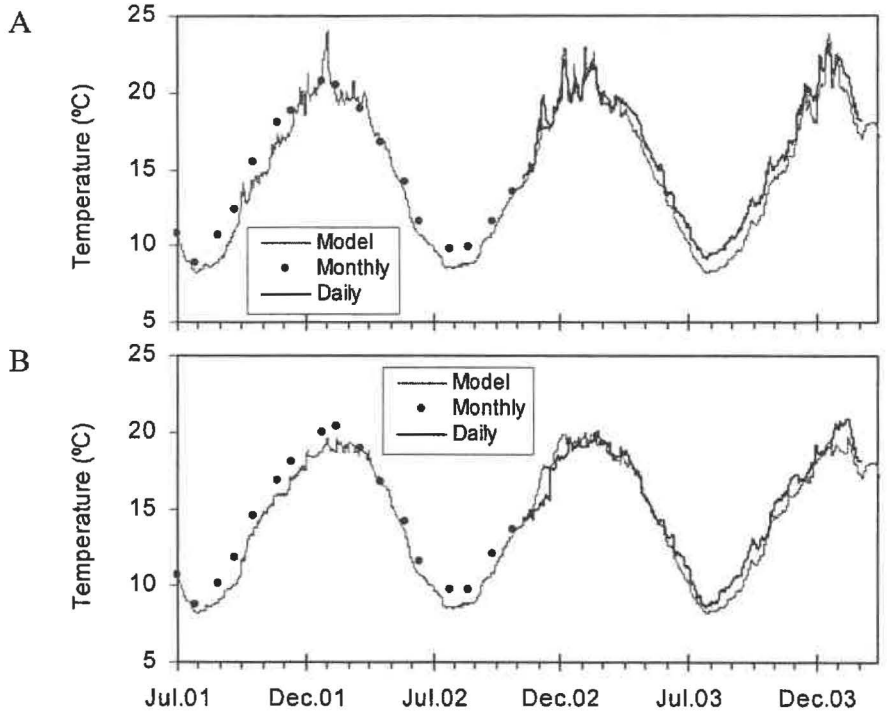

Figure 6.6: (A) Surface (depth 1.5 m) and (B) bottom (depth 19 m) water temperature in Lake Rotorua derived from model simulations, and monthly or daily observed temperatures, for the period Jul. 2001-Apr. 2004.

The DO, N and P parameters used in the ecological sub-model are listed in Table 6.5. Model simulations of surface DO concentration compared well with field measurements (Fig. 6.7), with a mean difference of 0.66 ± 0.81 mg L^{-1} over the study period (R value > 0.6, Table 6.3). Concentrations of DO were over-estimated by the model in bottom waters (mean 0.77 ± 1.77 mg L^{-1}), particularly during stratification events (Fig. 6.7).

Table 6.5: Dissolved oxygen (DO), nitrogen (N) and phosphorus (P) parameters used in CAEDYM.

Parameter	Symbol	Unit	Value
DO parameters			
Temperature multiplier for sediment oxygen demand	v_{OP}	dimensionless	1.08
Half saturation constant for sediment oxygen exchange	K_{SOs}	mg L^{-1}	3
Static sediment oxygen exchange rate	R_{SOs}	g m^{-2} d^{-1}	2.8
N parameters			
Denitrification rate coefficient	K_{oN2}	d^{-1}	0.5
Half saturation constant for denitrification	K_{N2}	mg L^{-1}	5
Temperature multiplier for denitrification	v_{N2}	dimensionless	1.08
Nitrification rate coefficient	K_{oNH}	d^{-1}	0.01
Half saturation constant for nitrification	K_{NH}	mg L^{-1}	1
Temperature multiplier for nitrification	v_{NH}	dimensionless	1.08
Maximum potential sediment nitrogen release rate	S_{mpN}	g m^{-2} d^{-1}	0.28
Maximum potential transfer of labile PON to DON	$PON_{L\ Max}$	d^{-1}	0.002
Maximum potential transfer of refractory PON to DON	$PON_{R\ Max}$	d^{-1}	0.0005
Maximum potential transfer of labile DON to NH_4	$DON_{L\ Max}$	d^{-1}	0.0025
Maximum potential transfer of refractory DON to NH_4	$DON_{R\ Max}$	d^{-1}	0.005
P parameters			
Maximum potential sediment phosphorus release rate	S_{mpP}	g m^{-2} d^{-1}	0.08
Maximum potential transfer of labile POP to DOP	$POP_{L\ Max}$	d^{-1}	0.005
Maximum potential transfer of refractory POP to DOP	$POP_{R\ Max}$	d^{-1}	0.005
Maximum potential transfer of labile DOP to PO_4	$DOP_{L\ Max}$	d^{-1}	0.04
Maximum potential transfer of refractory DOP to PO_4	$DOP_{R\ Max}$	d^{-1}	0.005

Simulations of SRP and TP captured not only the observed increases in hypolimnion P during stratification, but also the inter-annual variability (Fig. 6.8, $R > 0.6$, Table 6.3). In surface waters, model simulations tended to underestimate SRP and TP concentrations, particularly during stratification or immediately after water column mixing (Fig. 6.8, Table 6.3). Simulations of NH_4 in the bottom waters were also reproduced well by the model (Fig. 6.9), but NO_3 concentrations were slightly under-estimated in surface waters during summer, and over-estimated in bottom waters in summer 2001-02 (Table 6.3). Model simulations of TN showed little reduced variability relative to field measurements (Fig. 6.9).

In model simulations, concentrations of DO in the bottom waters during stratification were not critical for the release of dissolved nutrients from the sediments during stratification events. For example, in summer 2001-02, when the lake was stratified on three occasions for periods of 11 to 20 days, increases in SRP and NH_4 concentrations occurred even when DO concentrations remained greater than 5 mg L^{-}

^{1}, with the magnitude of nutrient increase dependent on the duration of each event rather than DO *per se* (Fig. 6.10). The onset of stratification and subsequent bottom water anoxia were characterised by calm conditions, with mean daily wind speeds of up to 4.7 m s^{-1} observed on the day prior to each of the three events in 2002 but mean daily wind speeds during stratification of only 3.3 m s^{-1} (Fig. 6.10).

Total chl-*a* concentrations in surface waters were reproduced relatively well by model simulations, which captured both the seasonal and inter-annual variability observed in the field data (Fig. 6.11). Over the whole period (Jun. 2001 - Apr. 2004), mean monthly concentrations of total chl-*a* (± SD) in the surface-mixed layer (depth integrated, 0-8 m) were 30.9 ± 8.9 μg L^{-1} in summer (Dec.-Mar.) and 17.5 ± 9.2 μg L^{-1} in winter (Jun.-Sep). Daily means of total chl-*a* concentration simulated by the model in the surface-mixed layer over the same time period were 24.4 ± 5.2 μg L^{-1} in summer and 17.1 ± 3.1 μg L^{-1} in winter. The collection of monthly field measurements during summer generally coincided with the presence of large bloom events.

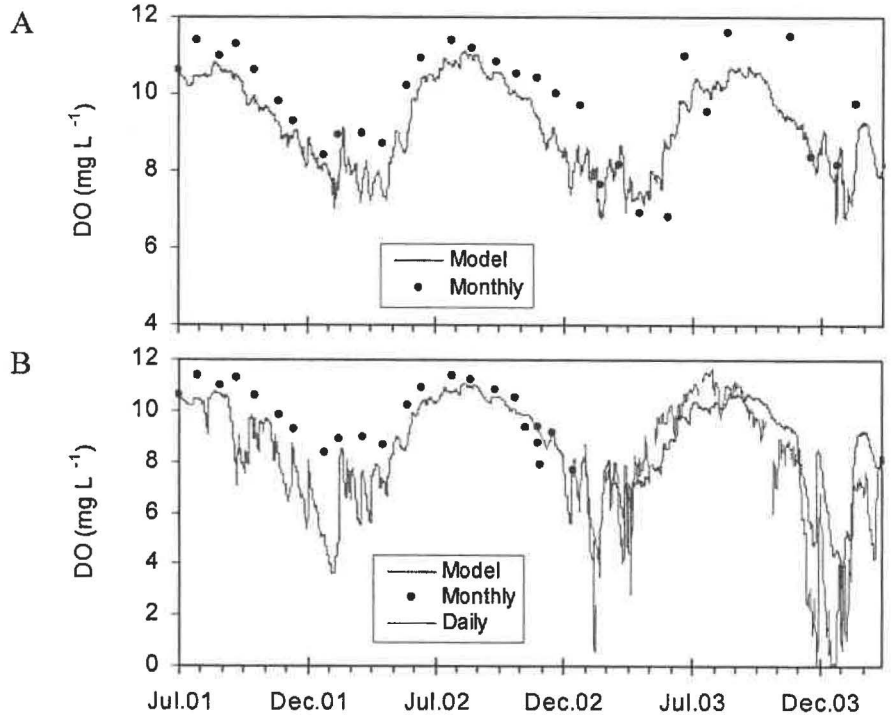

Figure 6.7: (A) Surface (depth 1.5 m) and (B) bottom (depth 19 m) dissolved oxygen concentrations in Lake Rotorua derived from model simulations, and monthly or daily observed values, for the period Jul. 2001-Apr. 2004.

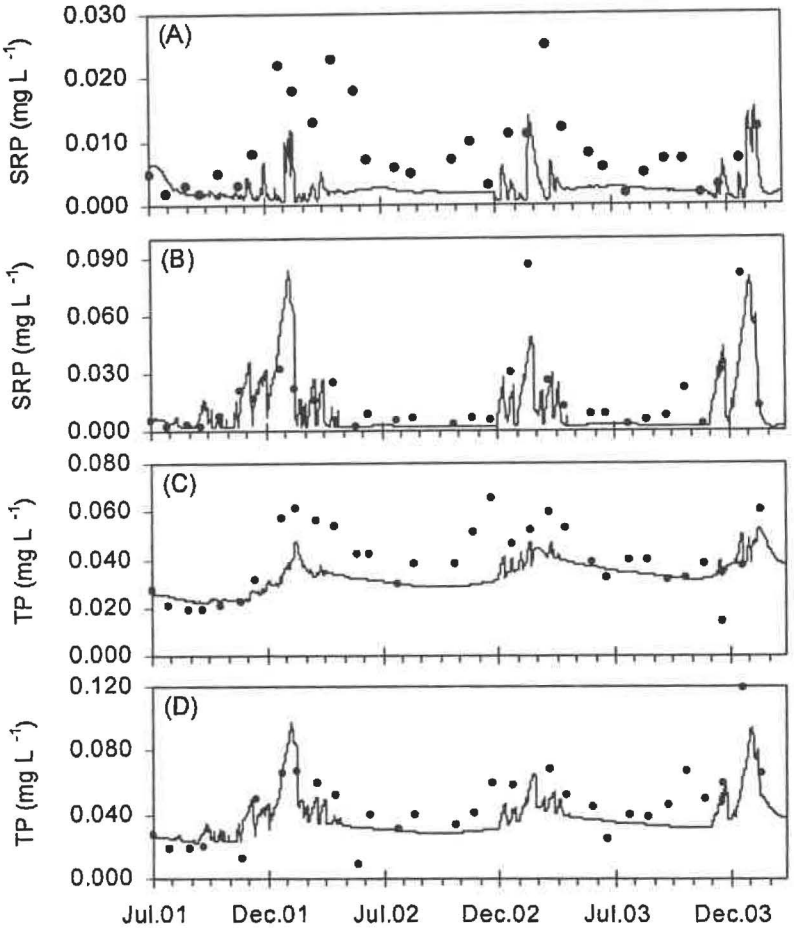

Figure 6.8: Comparison between Lake Rotorua model simulations (line) and monthly field measurements (points) for soluble reactive phosphorus (SRP) concentrations in (A) surface waters (depth 1.5 m) and (B) bottom waters (depth 19 m), and total phosphorus (TP) concentrations in (C) surface waters and (D) bottom waters, from Jul. 2001-Apr. 2004. Note surface and bottom water concentrations are on different scales.

In the model simulations during summer, 78 % of the phytoplankton biomass (i.e. represented by chl-*a*) was represented by cyanobacteria and 22 % by diatoms and other non-buoyant phytoplankton species (Fig. 6.11). In winter, cyanobacteria represented 60 % and other species 40 %, of the total chl-*a* concentration. During summer, cyanobacteria biomass increased in the surface waters, particularly during stratification events, with a mean daily difference in concentration between the surface and bottom waters of 32 %. Concentrations of cyanobacteria were up to 67 % higher in the surface waters on some days (2 Feb. 2002), and reached values of up to 38 μg chl-*a* L^{-1} (19 Jan. 2004).

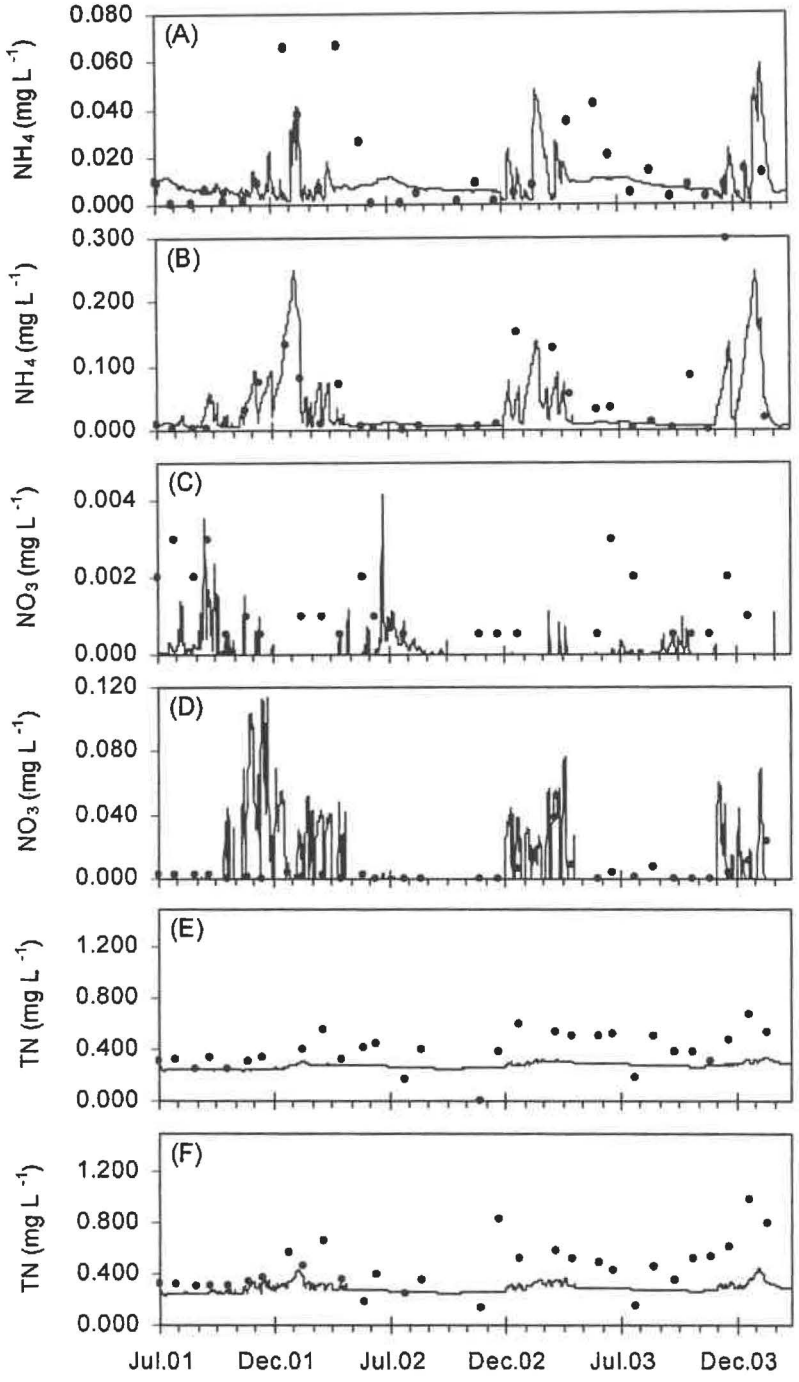

Figure 6.9: Comparison between Lake Rotorua model simulations (line) and monthly field measurements (points) for ammonium (NH_4) concentrations in (A) surface waters (depth 1.5 m) and (B) bottom waters (depth 19 m), nitrate concentration (NO_3) in (C) surface waters and (D) bottom waters, and total nitrogen concentration (TN) in (E) surface waters and (F) bottom waters, from Jul. 2001 to Apr. 2004. Note surface and bottom water concentrations are on different scales.

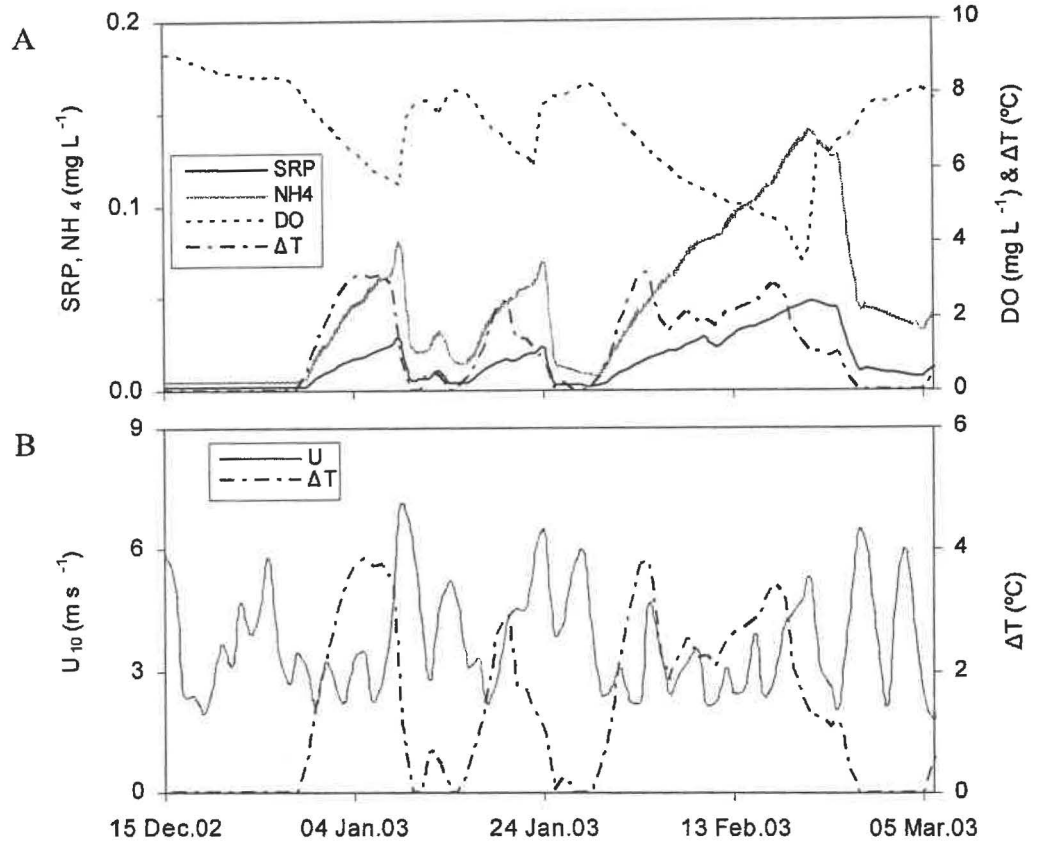

Figure 6.10: (A) Daily simulations of bottom water (depth 19 m) dissolved oxygen, soluble reactive phosphorus (SRP) and ammonium (NH_4) concentration, and simulated daily mean temperature difference (ΔT) between surface (depth 1 m) and bottom (depth 19 m) water, and (B) mean daily wind speed (U_{10}) at a reference height of 10 m from Rotorua Airport climate station, and ΔT, during three stratification events between 15 Dec. 2002 and 15 Mar. 2003.

Increases in cyanobacteria density in model simulations occurred at the onset of stratification, and before dissolved nutrient concentrations released from the sediments during stratification were circulated through the water column (Fig. 6.12). During stratification, concentrations of diatoms and other species in the surface-mixed layer generally decreased while cyanobacteria concentrations continued to increase, at rates of up to 4.9 μg chl-*a* L^{-1} day^{-1} (18 Jan. 2003, Figs. 6.11 and 6.12), declining only during partial-mixing events such as that observed on 7. Feb. 2003 (Fig. 6.12). After breakdown of stratification, surface cyanobacterial densities declined, and the large increases in SRP and NH_4 concentrations through the water column began to decline rapidly in association with increases in concentrations of diatoms and other species in surface waters (Fig. 6.12). Maximum rates of increase of diatoms and other species after stratification were 2.9 μg chl-*a* L^{-1} day^{-1} (2 Feb. 2002) (Fig. 6.12).

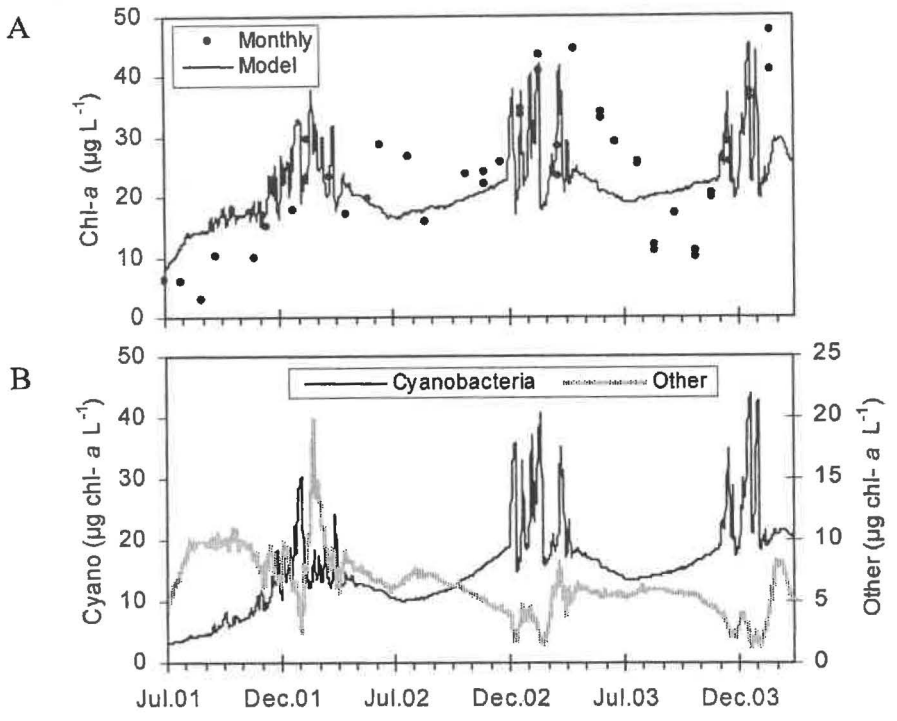

Figure 6.11: (A) Comparison between model simulations (line) and monthly field measurements (points) for chlorophyll *a* (chl-*a*) in the surface waters (depth 1.5 m) of Lake Rotorua and (B) model simulations of cyanobacteria (Cyano) and diatoms plus chlorophytes (other), expressed as chlorophyll *a* concentration, in the lake surface waters, from Jul. 2001to Apr. 2004.

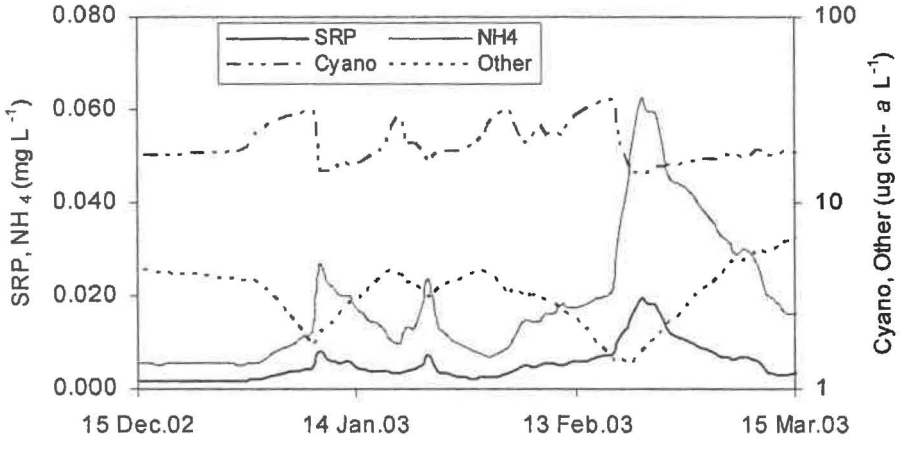

Figure 6.12: Model simulations of daily concentration of soluble reactive phosphorus (SRP), ammonium (NH_4), cyanobacteria (Cyano) and diatom and other species (Other) in the surface-mixed layer (depth integrated, 0-8 m), during three stratification events between 15 Dec. 2002 and 15 Mar. 2003.

Table 6.6: Daily mean (± standard deviation) depth integrated (0-8 m and 15-20m) concentrations of dissolved oxygen (DO), nutrients (SRP, TP, NH_4, NO_3, TN) and cyanobacterial chlorophyll *a* (Cyano) for summer (Dec.-Mar.) between Dec. 2001 and Mar. 2004, at current levels and those predicted to result from a 47 % reduction in external and internal nutrient loading.

Lake depth	Variable	Units	Current	External	Internal
Surface	DO	mg L^{-1}	7.9 ± 0.7	7.9 ± 0.7	7.8 ± 0.7
	SRP	mg L^{-1}	0.007 ± 0.006	0.006 ± 0.006	0.004 ± 0.003
	TP	mg L^{-1}	0.039 ± 0.007	0.038 ± 0.007	0.026 ± 0.003
	NH_4	mg L^{-1}	0.022 ± 0.020	0.022 ± 0.021	0.011 ± 0.009
	NO_3	mg L^{-1}	0.004 ± 0.006	0.000 ± 0.001	0.004 ± 0.006
	TN	mg L^{-1}	0.293 ± 0.024	0.287 ± 0.026	0.195 ± 0.015
	Cyano	µg chl-a L^{-1}	18.9 ± 6.1	20.0 ± 6.4	15.7 ± 3.5
Bottom	DO	mg L^{-1}	6.9 ± 1.4	7.0 ± 1.4	7.0 ± 1.3
	SRP	mg L^{-1}	0.019 ± 0.018	0.015 ± 0.015	0.012 ± 0.010
	TP	mg L^{-1}	0.047 ± 0.014	0.043 ± 0.011	0.030 ± 0.006
	NH_4	mg L^{-1}	0.057 ± 0.053	0.055 ± 0.049	0.029 ± 0.024
	NO_3	mg L^{-1}	0.020 ± 0.025	0.002 ± 0.004	0.016 ± 0.020
	TN	mg L^{-1}	0.315 ± 0.035	0.294 ± 0.033	0.207 ± 0.025
	Cyano	µg chl-a L^{-1}	12.8 ± 4.9	13.7 ± 5.1	11.2 ± 4.1

6.3.4 Management scenarios

Concentrations of SRP in surface waters showed the greatest reduction in model simulations when internal nutrient fluxes were reduced by 47 % compared with the equivalent external load reductions (Fig. 6.13). Mean daily summer (Dec.-Mar.) SRP concentrations in the surface-mixed layer (depth integrated, 0-8 m) over the whole model period (Jul. 2001- Mar. 2004) declined by 32 % in simulations with internal load reduction, compared with only 12 % for simulations of external load reduction (Table 6.6). Ammonium concentrations behaved similarly to SRP, with the largest decrease in surface waters also observed in simulations with internal load reductions (mean 47 %) and little difference from external load reductions (3 %) (Table 6.6). In bottom waters (depth integrated > 15 m) concentrations of SRP and NH_4 decreased by 39 and 50 %, respectively, in simulations of internal load reductions over the entire period (Table 6.6). Mean daily concentrations of NO_3 in bottom waters in summer decreased by 90 % in simulations of external load reduction (Table 6.6).

Surface water concentrations of cyanobacteria also showed the greatest decrease in model simulations when internal nutrient fluxes were reduced (Fig. 6.14). A decline of up to 54 % from the current biomass was observed on some days in summer (e.g., 2 Feb. 2002), with the largest daily decreases typically most evident during

stratification events (Fig. 6.15). Mean daily summer cyanobacteria biomass in the surface-mixed layer over the whole model period (Jun. 2001- Mar. 2004) declined by 17 % in simulations of internal load reduction, compared with a 5 % increase in simulations of external load reduction (Table 6.6). Mean daily total chl-*a* concentration declined by 33 % in the surface-mixed layer with internal load reductions, but only 6 % reduction with external load reductions.

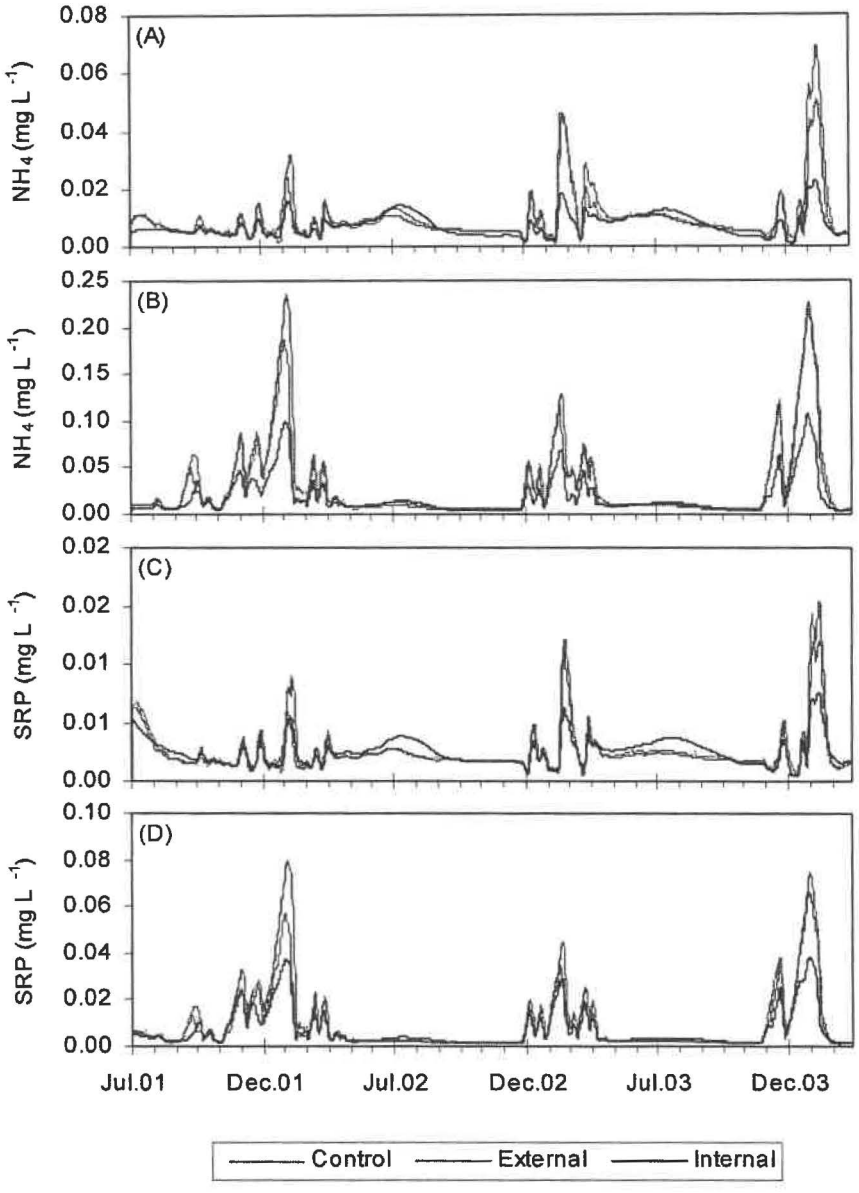

Figure 6.13: Comparisons between model simulations of current lake status (control), 47 % external nutrient load reduction (External) and 47 % reduction in sediment nutrient fluxes (Internal) for concentrations of soluble reactive phosphorus (SRP) in (A) surface waters (depth 0.5 m) and (B) bottom waters (depth 19 m), and concentration of ammonium in (C) surface waters and (D) bottom waters, from Jul. 2001 to Apr. 2004.

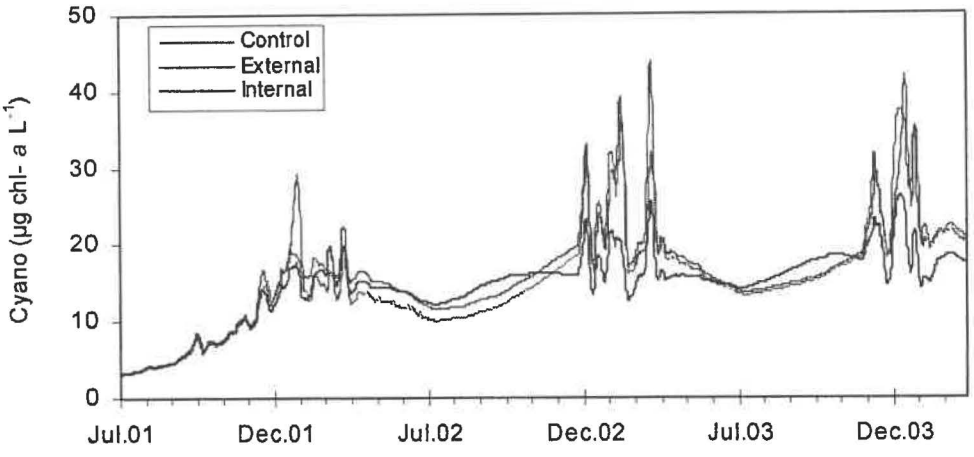

Figure 6.14: Comparisons between model simulations of current lake status (control), 47 % external nutrient load reduction (External) and 47 % reduction in sediment nutrient fluxes (Internal) on cyanobacteria (Cyano) in the surface waters (depth 0.5 m), expressed as chlorophyll *a* concentration, from Jul. 2001 to Apr. 2004.

6.4 Discussion

6.4.1 External loads

The high external nutrient loads to Lake Rotorua (34 t TP yr^{-1} and 536 t TN yr^{-1}) were associated predominantly with the 9 major inflows, which contributed 64 % of the total flow and approximately 70 % of the total N and P loads to the lake. The large contribution of ungauged inflows, estimated to represent 19 % of total flow and c. 21 % of the total nutrient load, highlights the importance of potentially large groundwater and ungauged inflows to the nutrient balance of this lake. However, further research on the groundwater flow rates and associated nutrient loading rates to the lake would be useful to validate these estimates. The 17 minor geothermal and coldwater inflows contributed relatively little to the total nutrient load in comparison to major inflows. While atmospheric deposition may represent an important source of nitrogen to lakes in the Northern Hemisphere (e.g. Hamilton et al., 2002), its contribution to the nutrient budget of this study (1.2 t TP yr^{-1} and 30 t TN yr^{-1}) was relatively unimportant compared with other sources.

External loads of TP contributed by the nine major inflows have remained largely unchanged between 1976 and 2002 (Rutherford, 2004), which indirectly supports earlier findings (Timperley, 1983) that due to the volcanic nature of the catchment with rhyolitic aquifers, 95 % of P associated with the mostly spring-fed inflows to

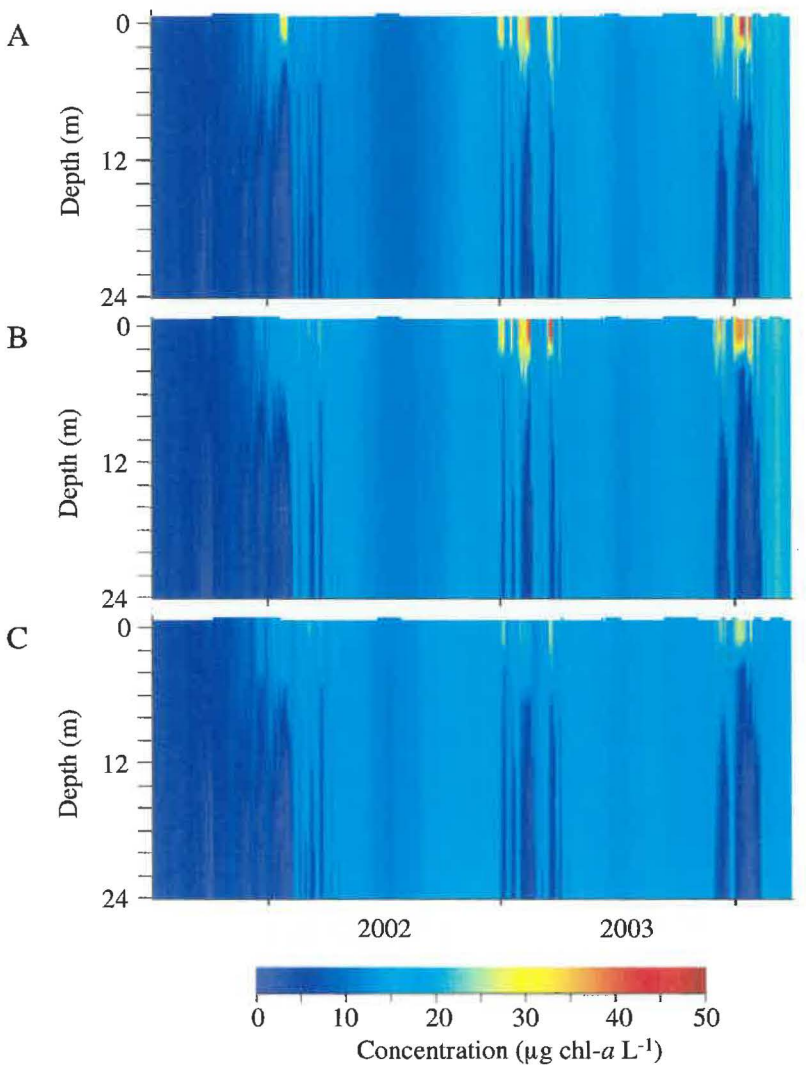

Figure 6.15: Comparisons between model simulations of (A) current lake status, (B) 47 % external nutrient load reduction and (C) 47 % reduction in sediment nutrient fluxes on cyanobacteria biomass, expressed as chlorophyll *a* concentration, from Jul. 2001 to Apr. 2004.

Lake Rotorua is derived from natural sources. Estimates of external TP loads to Lake Rotorua for the periods 1976-1978 (Hoare, 1987), 1984-85 (Rutherford, 1989) and in 2002 (Rutherford, 2004) derive similar estimates of c. 34 t yr^{-1}, excluding discharges of treated sewage. Comparisons of external TN loads associated with the nine major inflows between the current study and Hoare (1987) revealed a 33 % increase in NO_3 loads since 1976, equating to 77 t yr^{-1}. These comparisons also show that total N loads have increased in six of the nine major inflows: Awahou, Hamurana, Ngongotaha, Puarenga, Waingaehe and Waiohewa Streams. The largest increase

occurred in the Puarenga Stream, where current NO_3 loads of 49 t yr^{-1} are over four times higher than estimates by Hoare (1987).

It is suggested that this increase is associated with diversion of wastewater from Lake Rotorua to spray irrigation into Whakarewarewa Forest, situated in the Puarenga catchment, and is also associated with the highly porous nature of volcanic soils in the Rotorua catchment. Increases in NO_3 loads of between 23 and 50 % were also observed in the largest inflows, the Hamurana and Awahou, both of which are predominantly spring-fed by large groundwater aquifers (Hoare, 1980). Over 94 % of the NO_3 concentration in the 'young' (< 40 years) groundwater is derived from intensive agricultural practices in the catchment, and NO_3 concentrations associated with these discharges are expected to increase by a factor of three once discharge reaches a steady state after 2065 (Morgenstern et al., 2004).

6.4.2 Model simulations

The model simulations of water quality in Lake Rotorua represented the complex polymictic dynamics and rapid transitions of nutrients and phytoplankton in the lake, including the timing and duration of stratification events and increases in SRP and NH_4 concentrations in bottom waters. The model also captured the inter-annual variability associated with stratification, including differences in bottom water nutrient concentrations observed in the field data between the three years. However, statistical comparisons between model simulations and monthly field measurements suggest that the model is unable to capture varying proportions of the variability observed in the field data, particularly for surface concentrations of NH_4 and NO_3, although errors are within in the range reported elsewhere (Arhonditsis and Brett, 2005) and are attributable to some extent to the relatively low concentrations of these nutrients in the surface mixed layer.

A previous application of an earlier version of the DYRESM model to Lake Rotorua (Rutherford et al., 1996) was not able to reproduce the duration and strength of thermal stratification as precisely as in this study. The reasons for the improvement in the current model application may be related to more accurate alignment of model output with the time when samples were collected, prescription of a geothermal heat flux from the bottom sediments, and the feedback of phytoplankton biomass to the

light attenuation coefficient as the earlier model application did not include a water quality module. Model simulations of water column temperatures were found to be slightly cooler than field observations. Gal et al. (2003) suggest that the DYRESM model is highly sensitive to long wave radiation inputs, and together with the limited work on the benthic boundary layer and internal mixing parameters, may have introduced some error into predictions of metalimnion and bottom water temperatures.

Model simulations suggest that development of cyanobacterial blooms commonly occurs when chl-*a* concentrations exceed 30 $\mu g\ L^{-1}$ in surface waters, coinciding with the onset of stratification. Concentrations of cyanobacterial chl-*a* generally continued to increase over the duration of stratification in the model simulations, suggesting that cyanobacterial growth was not severely constrained by nutrient availability at this time. This observation suggests that interactions amongst light limitation and mixing depth may be important in the short-term in regulating biomass of cyanobacteria. This supports the findings of phytoplankton bioassay experiments presented in Chapter 3, which suggest that both light and nutrient limitation are important regulating factors in the phytoplankton community assemblage and biomass.

Parameters used to characterise the two groups of phytoplankton represented in the model were prescribed using literature values and represent only 'average values' over the assemblage of phytoplankton species represented by the two groups. For example, the parameters used to specify phytoplankton growth rates, nutrient uptake rates, nutrient storage, light responses and settling rates may be expected to vary between species and lakes, as well as with time for individual species (e.g. Kirk, 1997; Reynolds, 1997). In Lake Rotorua, cyanobacteria populations were dominated at various times by *Anabaena planktonica* or *Microcystis aeruginosa*, and these species responded differently to N and P enrichment bioassays (Chapter 3). Model simulations appeared to be most sensitive to minimum and maximum internal P and N concentrations within individual phytoplankton cells, and while it is not possible to conduct a sensitivity analysis over all phytoplankton parameters described in the model (Romero et al., 2004), measurements of these parameters for the dominant phytoplankton species in Lake Rotorua may improve the model.

Comparisons between model simulations of external and internal nutrient load reduction clearly indicate that sediment nutrient fluxes are the dominant source of nutrients to Lake Rotorua under present loading rates and trophic status. For nutrient concentrations in the surface-mixed layer over the summer period, a 47 % reduction in sediment nutrient release rates was between 20 and 30 % more effective in reducing SRP and TP concentrations, and between 30 and 50 % more effective in reducing NH_4 and TN concentrations, than an equivalent 47 % reduction in external loads. Sediment nutrient release rates specified in the model represent measured values derived from experiments conducted in the lake within the simulation period (Chapter 5), and provide critical data for refining the accuracy of simulations.

Reductions in total chl-*a* concentration and cyanobacterial biomass (33 and 17 %, respectively) with a 47% reduction in internal nutrient load were substantially larger than for the same reduction in external load. The 6 % increase in summer cyanobacteria biomass observed in simulations of external nutrient load reduction suggests that the large reduction in NO_3 concentrations derived from external inputs may have important implications for altering redox potential at the sediment-water interface, and therefore affecting sediment nutrient release rates. A large reduction in NO_3 concentrations may deplete electron acceptors relative to SRP desorption processes, and subsequently enhance rates of sediment SRP release to the overlying water column (Kleeberg and Kozerski, 1997). However, it is uncertain whether high concentrations of NO_3 derived from external sources reach the bottom waters of Lake Rotorua, or whether this is a limitation of the current model.

While our model simulations demonstrate the current dominance of internal loads to lake water column nutrient concentrations and cyanobacteria biomass in Lake Rotorua, only a significant and prolonged reduction in external loads will reduce internal nutrient recycling in Lake Rotorua. The high external nutrient loads to the lake, coupled with a moderate lake surface area to volume ratio and a water residence time of 1.5 years, suggest that the lake will continue to remain eutrophic under present and reduced loading rates.

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Chapter 7: Conclusions

7.1 Research summary

The magnitude and dynamics of internal nutrient loading are of critical importance for management of eutrophic lakes. Internal nutrient loads sustain elevated water column nutrient concentrations and in turn, high rates of phytoplankton productivity. This study has provided insights into the importance of internal nutrient fluxes to Lake Rotorua, the spatial and temporal variability of these fluxes, as well as the dominant nutrient cycling pathways. The study also highlights the need for examining both nitrogen (N) and phosphorus (P) when assessing phytoplankton nutrient limitation in polymictic lakes that may be subject to high temporal variability in sediment nutrient fluxes. The results presented in this thesis have important implications for the management of other shallow eutrophic lakes, providing insights into the dynamics of internal loads and how they may delay lake restoration efforts.

In Chapter 2, the contribution of sediment release rates of P to the overlying water column in Lake Rotorua was described during a summer stratification event using changing hypolimnion P concentration and changes in mass of P due to diffusion across the thermocline, partial mixing events, inflows, settling and regeneration. A simple mass balance model captured the dominant P fluxes in this system and allowed determination of an integrated release rate for the lake bed beneath the thermocline. The model indicated that sediment P release rates were substantial, though within the range of releases observed in eutrophic lakes elsewhere. The results of a sensitivity analysis conducted on the parameter values for P settling and regeneration suggest that better determination of these parameters, specifically for Lake Rotorua, will improve the accuracy of the results. While more accurate determination of diffusion rates across the thermocline may also improve the model, due to the relatively short duration of stratification events, diffusion is not likely to represent an important source of nutrients to the surface-mixed layer in Lake Rotorua.

Chapter 3 provides information on nutrient limitation of Lake Rotorua phytoplankton based on three 4-day *in situ* incubation experiments conducted in summer 2002-3.

While the use of *in situ* bio-assays was an attempt to conduct the experiments under the natural conditions normally observed in the lake, responses of the phytoplankton were difficult to interpret, and often not significantly different between treatments. However, this study clearly demonstrated that while the phytoplankton community increments to both N and P additions were more marked, individual taxa, including the cyanophyceae and chlorophyceae, and species within these taxa (e.g. *Anabaena planktonica* and *Microcystis aeruginosa*), responded differently to N or P additions, suggesting that the phytoplankton community in Lake Rotorua is co-limited by both nutrients.

The decrease in phytoplankton nutrient demand observed in the incubations after a breakdown in summer stratification suggests that internal nutrient fluxes may be important regulators of phytoplankton biomass over the summer period. Frequent mixing events may allow opportunities for luxury P uptake, particularly for cyanobacteria species such as *Microcystis aeruginosa*. In part, this is supported by the lake-wide model application in Chapter 6, which demonstrates a reduction in summer cyanobacteria biomass in association with reduced sediment nutrient release rates, but not reduced external loading rates. A better understanding of luxury nutrient uptake by individual phytoplankton species may assist interpretation of species-specific nutrient limitation in this lake. Certain heterocystous cyanobacteria, including *Anabaena planktonica*, also have the ability to fix atmospheric nitrogen during N limitation, although in this study very few filaments were observed to be heterocystous.

Model simulations conducted on the incubations in Chapter 3, used to examine the interacting effects of light and nutrients, suggest that light limitation was more frequent than limitation by N or P. Application of the lake-wide model in Chapter 6 also showed different taxa responses, with a reduction in diatoms and chlorophytes during cyanobacteria blooms in the surface-mixed layer during stratification events. Additional study to elucidate the nature of interactions amongst light and nutrient limitation would improve knowledge of the regulating factors in phytoplankton community assemblages and biomass in Lake Rotorua.

The large sedimentation rates of total particulate material to the benthos that were presented as observations in Chapter 4 suggest that sedimentation forms an important component of the internal nutrient cycle in Lake Rotorua. Net sedimentation rates, measured seasonally at three sites, were generally highest in summer, which may have important implications for controlling the magnitude and seasonality of decomposition rates, and therefore nutrient release rates from the sediments back into the overlying water column. Differences between net retention of N and P in Lake Rotorua, based on a lake-wide nutrient mass balance, and gross fluxes of N and P across the sediments measured with sedimentation traps, indicate that N and P are recycled several times between the sediments and water column before ultimate burial or loss via Ohau Channel outflow. The much higher estimates of recycling for P than for N suggest that denitrification in the sediments may also represent an important loss process for N in the water column.

The use of sediment traps positioned at several depths in the water column at each site also allowed more detailed examination of the contribution of resuspension to the sedimenting flux. Gross sedimentation rates were characterised by increases in the fraction of particulate inorganic material, due to increasing mineral-bound P in association with resuspension. Resuspension was highest at the shallowest site (depth 7 m), where the fraction of total particulate matter (TPM) derived from resuspension was estimated to be up to 71 %. There is potential for significant lake-wide effects of resuspension as 34 % of the lake area is less than 7 m deep. Horizontal transport of resuspended material from the littoral to pelagic zone is also important in this lake as up to 47 % of total particulate matter at the deepest site (depth 20 m) was contributed by resuspended material. Molar ratios of particulate organic carbon to particulate organic nitrogen were relatively invariant with water column depth, suggesting that mineralisation of resuspended particulates is not especially important in the water column.

In Chapter 5, release rates of soluble reactive phosphorus (SRP) and ammonium (NH_4) from the bottom sediments of Lake Rotorua to the overlying water column were found to be much greater than nutrients derived from inflows to the lake, suggesting that internal loads will delay improvements in lake water quality in the presence of reduced external loads. Nutrient release rates were measured seasonally

with *in situ* benthic chamber deployments at three sites in the lake. The similarity between SRP release rates derived from the chamber measurements and those estimated using changes in hypolimnion concentration, measured on one occasion during stratification, suggest that chamber measurements are indeed representative at the lake scale. Two release rates were observed for NH_4 in all chamber measurements, and it is uncertain if this is an artefact of chamber deployment or represents a natural response to changing dissolved oxygen concentration or bacterial productivity.

Release rates of SRP were largely independent of dissolved oxygen concentrations in overlying water of the chambers, indicating that SRP release is not only limited to stratification or deoxygenation events, but also represents a significant source of nutrients when the lake is mixed. Release rates of both NH_4 and SRP showed strong seasonal variability and were highest in summer chamber deployments, when phytoplankton biomass in the lake is greatest, and there is likely to be higher biological demand for nutrients. Release rates also varied between sites and the deepest site had the highest nutrient fluxes. This may have important implications for targeting specific areas of lake sediment for removal or capping as a management strategy to reduce internal nutrient loads.

In Chapter 6, a one-dimensional coupled hydrodynamic and ecological model was applied to Lake Rotorua to examine the relative importance of external and internal nutrients to water column nutrient concentrations and phytoplankton biomass, particularly cyanobacteria. External nutrient loads were determined for a total of 27 inflows, with high external loading rates associated primarily with nine major inflows. Model simulations of water column temperature and SRP and NH_4 concentrations compared well with field observations, and the model captured the complex nature of stratification and sediment nutrient fluxes associated with mixing and destratification events in polymictic Lake Rotorua. Scenarios of external and internal load reductions indicate that sediment nutrient fluxes are currently more important in influencing the high observed nutrient concentrations and cyanobacteria biomass in surface waters than external nutrient loads, due to coincidence of stratification and major nutrient releases with elevated cyanobacterial biomass in summer. This suggests that reducing internal loads, either through sediment dredging,

capping or flocculants, is a more effective management strategy than external load reductions under the present loading rates.

In summary, this study demonstrates the importance of internal nutrient loads in sustaining the current eutrophic status of Lake Rotorua. High external loading rates, coupled with high rates of organic matter sedimentation and sediment nutrient release, suggest that there may be little change to the current water quality status of Lake Rotorua, which is characterised by blooms of cyanobacteria in summer and deoxygenation of bottom waters during summer stratification events of more than a few days. The results of this study emphasise the importance of conducting experimental measures of internal nutrient releases, and provide important insights into the complex dynamics of nutrient recycling in shallow, polymictic, eutrophic lakes.

7.2 Recommendations for future work

Indirect estimates of sediment resuspension from TPM in vertically resolved sediment traps has indicated that this process is a major contributor of particulate nutrients in Lake Rotorua. While the amount of TPM in traps was not significantly correlated with mean wind speed over the duration of the four trap deployments, there may be short-term relationships between sediment resuspension and wind speed that were not resolved in this study. Sediment trap deployments on a daily timescale may provide a better understanding of sediment resuspension frequency, duration and magnitude, and associated nutrient fluxes in the lake. A delineation of zones of erosion and deposition may also provide important insights into the spatial variability of sediment resuspension events. However, direct measurements of resuspension may ultimately produce better insights into the dynamics of sediment resuspension, and other techniques such as use of radionuclides (Bloesch, 1995), direct measurements of suspended sediment and nutrient concentrations at high frequency (Bloesch, 1995), and determination of dissolved nutrient remobilisation from sediment porewaters into the overlying water column during resuspension (e.g. Søndergaard et al., 1992) could be investigated.

Release rates of SRP under aerobic water column conditions, as described in this study in Chapter 5, may be associated with sediment anoxia due to high rates of organic matter decomposition at the sediment water interface (Marsden, 1989; Kleeberg and Kozerski, 1997). Micro-profiling of dissolved oxygen concentrations through the benthic boundary layer and into the sediments would help to determine if anoxia is the underlying mechanism mediating sediment SRP release in the presence of an aerobic water column. Quantification of organic matter composition in the sediments at all sites concurrently with measurements of nutrient release may reveal important relationships between the amount of organic material and the magnitude of release. This would provide a better understanding of the mechanisms associated with SRP release in particular, and help to define the relationships and role of concentrations of organic matter, dissolved oxygen, nitrate and metabolic activities of micro-organisms. Release rates of dissolved organic P and N from the bottom sediments may also provide an important contribution to internal loading in this lake, and the role of this component in both the water column and sediments should be examined further.

The mechanisms leading to two apparent rates of ammonium release observed in the benthic chamber experiments described in Chapter 5 also require further examination. While it is possible that NH_4 release rates may have been enhanced by isolation of the sediments or with porewater displacement associated with the chamber placement, there was no evidence of this phenomenon for SRP. Sediment core incubations conducted in the laboratory under precisely controlled oxic or anoxic conditions, or with sterilised sediment cores to remove bacterial activity, may provide important insights into the dynamics of NH_4 release, the role of bacterial flora, and whether the observed release rates were indeed an artefact of the chamber deployment.

The validated one-dimensional hydrodynamic and ecological model used in the results presented in Chapter 6 enabled an examination of internal versus external nutrient loads on water column nutrient and phytoplankton dynamics. Use of this model could be extended to examine other nutrient reduction scenarios to assist with providing direction in lake restoration efforts. The model could be applied to a more detailed examination of external load reductions through individual stream diversions or treatment, or internal load reductions through scenarios to examine sediment

dredging, capping or flocculants, by adjusting bathymetry, sediment nutrient release or sedimentation rates, respectively, in the model input data. Modification of the model code relating to sediment nutrient releases would allow more detailed testing of internal and external load reduction strategies. This modification may be useful for the case where external and internal loads are reduced by identical amounts, as opposed to identical proportions. The model could also be used to examine increasing external nitrate loads associated with groundwater flows (Morgenstern et al., 2004) and the effects of climate change and different stratification regimes on cyanobacterial bloom formation (e.g. Huisman et al., 2004).

The ability of the model to accurately capture the complexity of the phytoplankton groups is largely dependent on the parameters used to describe individual species. While the phytoplankton parameters used in the current model application are derived largely from international literature sources, experimental determination of growth rates, nutrient uptake rates, minimum and maximum internal nutrient stores and irradiance parameters for individual species in Lake Rotorua would greatly improve the model predictive abilities. The use of a three-dimensional hydrodynamics model, coupled with current ecological model, may also be beneficial in examining the patchiness observed in the spatial distribution of phytoplankton biomass and cyanobacteria blooms (Ryan et al., 2005). The application of a three-dimensional model may also better address the spatial variability in sedimentation rates, resuspension processes, sediment nutrient release rates and inflow effects observed in Lake Rotorua in this study.

7.3 References

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