Trophic State in Canterbury Waterways

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

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Preface

This thesis investigates trophic state variation within Lake Forsyth and twenty one streams located in Canterbury, New Zealand. I have written this thesis as a set of three "stand-alone" scientific papers intended for publication, so that each chapter concerns a different facet of the topic.

The first chapter concerns how riparian conditions influence the trophic state of stream communities. The second chapter concerns how water quality parameters, weather and nutrients are linked with cyanobacterial bloom occurrence within Lake Forsyth. The third chapter compares the character of stream trophic state within the Canterbury region to national and international studies of stream trophic state.

There is some overlap between chapters one and three. To avoid repetition, I have referenced site descriptions, methods and figures in the third chapter to the first chapter. Publications resulting from this work will be multi-authored, reflecting contributions from others who assisted with the experimental design and field sampling. Specifically, Julie Edwards, Adrian Meredith, Tim Davie and other Environment Canterbury staff collected and contributed the Lake Forsyth water quality dataset; Elizabeth Graham and Katie McHugh assisted with the design and execution of sampling stream trophic state; and my supervisors, Angus McIntosh and Jon O'Brien contributed to study design, execution, analysis and writing. Although these people made significant contributions, the work is primarily my own and I will be first author on publications resulting from this work.

Abstract

Aquatic eutrophication is a serious global problem, associated with phytoplankton blooms, hypoxia, and loss of species. The objective of this thesis was to advance understanding of stream and lake eutrophication within Canterbury (South Island, New Zealand). I investigated three key questions: 1) How do riparian characteristics control stream trophic state, 2) how does stream trophic state in the Canterbury region compare to stream trophic state nationally and internationally, and 3) what factors control trophic state in Te Wairewa/Lake Forsyth. I measured rates of stream community metabolism in 21 Canterbury streams over a gradient of riparian canopy cover, and conducted a literature review of national and international studies of stream metabolism. I also examined the occurrence of cyanobacterial blooms in Te Wairewa in relation to water quality and weather from 17 years of measurements, and performed series of nutrient addition assays on the lake to assess nutrient limitation. I found that riparian characteristics strongly controlled stream trophic state by shading, thereby reducing photosynthetic productivity. This overwhelmed the effects of high nitrate concentrations, which increased primary production. Compared to national and international rates of stream metabolism, Canterbury streams were strongly heterotrophic, with low rates of autotrophic production. Catchment streams draining into Te Wairewa were unlikely to be the main source of nutrients supporting large cyanobacterial blooms. Instead, internal lake nutrient loading mechanisms associated with calm weather were likely to supply blooms. My results emphasize the importance of light limitation, nitrogen and heterotrophy in controlling stream trophic state, and nutrient supply and weather in controlling lake trophic state.

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"Water is life's mater and matrix, mother and medium.
There is no life without water."

Albert Szent-Gyorgyi

Chapter 1: Riparian control of stream trophic state through shading

ABSTRACT

Restoration of riparian vegetation is widely recommended to mitigate the adverse effects of agriculture on stream ecosystems, but there have been few assessments of how riparian conditions influence in-stream processes. To investigate the effect of riparian vegetation on in-stream vegetation, I measured community metabolism in 21 agricultural streams along a riparian vegetation gradient from closed canopied to open canopied, in the Canterbury region of New Zealand. Stream metabolism was measured using the single station open channel diel oxygen logging method. Oxygen re-aeration was assessed using both the propane injection and night-time regression methods. I found a gradient of trophic states ranging from oligotrophic to eutrophic across my sites. Gross primary production (P) ranged between 0.04 and 2.78 g O_2 m^2 day^{-1} and respiration (R) between 1.4 and 33.3 g O_2 m^2 day^{-1} . Streams were strongly heterotrophic with P:R values varying between 0.01 to 0.25. Although catchment land-use was positively correlated with production, respiration and the P:R ratio, riparian condition had a stronger effect on metabolic rates. Regressions of shading, and secondarily nitrate, best predicted stream production and P:R ratios. Respiration was best predicted by shading alone. My results highlight the primacy of riparian condition in controlling stream trophic state and the importance of riparian buffers as a tool to avoid stream eutrophication.

INTRODUCTION

Increases in the extent and intensity of agriculture have led to widespread and continuing degradation of stream health globally (Foley et al. 2005, Vorosmarty et al. 2010). Agricultural land can influence stream ecosystems by increasing stream concentrations of sediment, nutrients, microbes and pesticides, altering flow and reducing riparian and stream habitat (Allan 2004).

Agriculturally driven degradation of streams is often characterised by changes in stream trophic state (Young et al. 1999, Fellows et al. 2006, Von Schiller et al. 2008, Bernot et al. 2010). Trophic state is the amount of energy available for both autotrophic and heterotrophic activities within a community (Dodds et al. 2007), and energy available for both types of activities can be influenced by agriculture. Removal of riparian vegetation to create pasture or crop land boosts autotrophic production by increasing light available for photosynthesis (Hill et al. 1995), whereas heterotrophic respiration is decreased in agricultural streams due to reduced litter-fall (Young et al. 1999). Vegetation removal, tilling and stock pugging also increase erosion and sediment concentrations in stream water which support productive macrophyte beds (Barko 1991) but can also reduce light available for macrophyte and algal production (Davies-Colley et al. 1992, Young et al. 1996, Young et al. 1999). Increased concentrations of nutrients from non-point sources can stimulate photosynthetic growth (Rosemond et al. 1993, Mosisch et al. 2001) and increase respiration (Greenwood et al. 2007).

One strategy to mitigate the effects of agriculture on stream health is through riparian buffers. Suggested riparian buffer zones consist of grass or woody strips of varying thickness, planted close beside the channel (Lee et al. 2004, Mayer 2005, Craig et

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al. 2008). In New Zealand, riparian plantings can sometimes consist of native grasses, shrubs or flax, but more often consist of exotic pasture grasses or shrubs and trees (e.g. willow or mulberry). Planted riparian zones have the potential to protect stream health from agricultural influences by reducing excess inputs of sediment (Carver et al. 2006, Canfield et al. 2007) and nutrients (Hopkins et al. 2002, Craig et al. 2008, Kronvang et al. 2009), reducing stream temperature (Ebersole et al. 2003, Caissie 2006) and available light (Hill et al. 1995). However, where the effects of riparian plantings on stream communities have been evaluated, the success of these rehabilitation projects has been mixed, and dependent on stream specific factors such as up-stream influences, catchment geomorphology, land-use and the age and width of the buffering vegetation (Parkyn et al. 2003, Craig et al. 2008, Wilcock et al. 2009). Few direct evaluations of the effect of riparian vegetation on trophic state exist, despite the need to better understand how to manipulate in-stream conditions to reduce both in-stream eutrophication and the eutrophication of downstream environments.

Riparian vegetation may have a disproportional effect on the trophic state of stream ecosystems directly by affecting shading and organic matter inputs and indirectly by modifying landscape inputs. Several studies indicate important influences riparian vegetation has on metabolism of organic matter (Bott et al. 1985, Bunn et al. 1999, Young et al. 1999, Hagen et al. 2010). However, the relative importance of riparian vegetation has been difficult to isolate from catchment influences. For example Bunn and colleagues (1999) found a close association between canopy cover and algal production in the Mary River, Australia, but not in other rivers. They attributed this to impacts from intensive land use such as sediment, nutrients and salinity. Evaluation of riparian influence on trophic

state relative to catchment influence is necessary to properly assess the importance of riparian buffer zones in minimising agricultural effects.

In this study, I investigated the effect of riparian cover on stream trophic state in a survey of 21 agricultural streams in New Zealand. I hypothesized that riparian vegetation controls metabolic state by shading streams and introducing organic mater. I expected shading to reduce available light for photosynthesis, suppressing autotrophic production and reducing algal standing stocks. I also predicted organic matter inputs to increase heterotrophic respiration rates.

METHODS

Study area

I established sites on 21 stream reaches in the Canterbury region of the South Island, New Zealand (Figure 1). Streams in Canterbury flow through a diversity of temperate environments with varying geomorphology, flora, fauna, land use and riparian vegetation. The region has strong agricultural development, with extensive areas of land used for grazing livestock at varying densities (Taylor et al. 1997, MacLeod et al. 2006). Dairy, beef and sheep farming are common, with a lesser amount of cropping, horticulture and exotic plantation forestry. Areas of relatively pristine and regenerating native forest are also present in reserves. Riparian vegetation ranges from grass, short shrubs, hedges and exotic trees to evergreen native forest. In general riparian vegetation is patchy, and streams with continuous riparian vegetation on every tributary are extremely rare outside protected nature reserves or land used for commercial forestry.
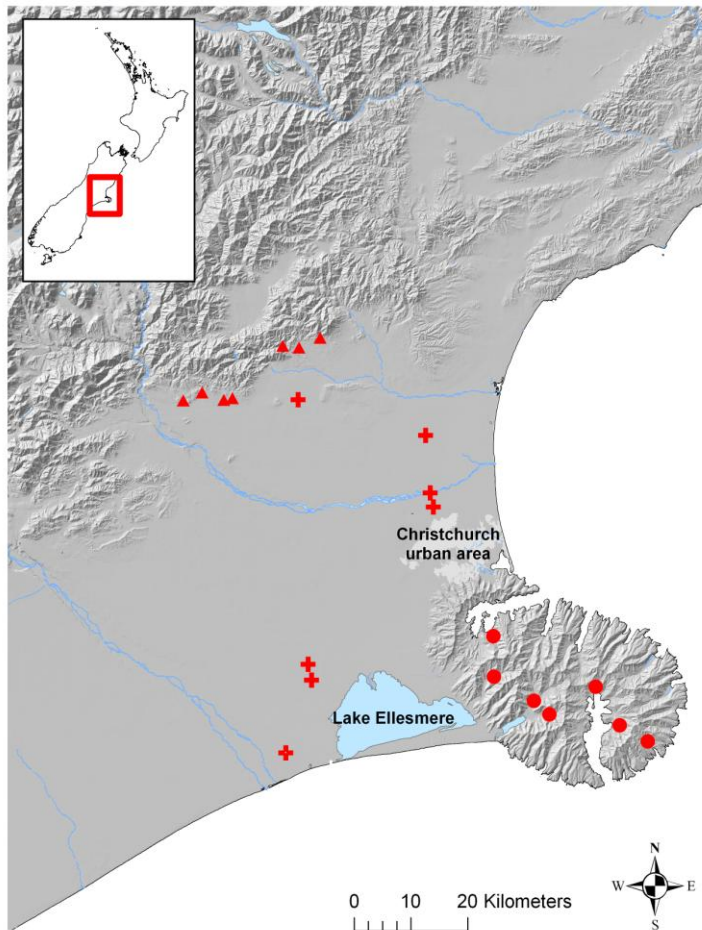
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Figure 1. My study area was the Canterbury region, South Island, New Zealand. We selected sites along a gradient of riparian condition in three sub regions, Canterbury Foothills (triangles) Canterbury Plains (crosses) and Banks Peninsula (circles).

Sites were selected to represent a gradient of riparian vegetation cover, from closed canopy to open canopied streams. Cobble bottom stream sites with a range of nutrient concentrations and varying intensities of catchment land-use were chosen where possible to avoid confounding the riparian gradient with a sediment, nutrient or land-use intensity gradient. Streams were sampled in the late summer of 2010 between February and April. I chose streams from three sub-regions, the Canterbury Plains, Banks Peninsula and Canterbury foothills, so as to capture the entire gradient in riparian condition each sub-region.

The Canterbury Plains sub-region is a flat, intensively agricultural area, located on gravel outwash plains east of the Southern Alps (Figure 1). Irrigation channels supplying these farms with water criss-cross the land. Streams are often spring-fed, with a low gradient. Very little native forest remains, and exotics such as pine (*Cupressus macrocarpa* and *Pinus radiata)*, gorse *(Ulex europaeus)*, blackberry (*Rubus fruticosus)*, broom (*Cytisus scoparius, Cytisus multiflorus* and *Teline monspessulana)* and grass (various species) are common riparian and inter-paddock species. The lack of any completely closed-canopied streams in this sub-region limited my ability to capture the whole gradient in riparian condition here.

Banks Peninsula is a hilly region of volcanic origin to the east of the plains. Most of the original forest has been removed, but in many places native forest is regenerating in stream gullies alongside introduced plant species (Harding 2003). Agricultural activities here are often less intensive than on the plains; however dairy farming, as well as sheep and beef farming, at moderate stocking densities occurs. Riparian vegetation varies from regenerated native forest with full canopy closure to open streams bordered with gorse and shrubs, occasional trees only, or only grass.

The foothills sub-region rises to the west of the Canterbury plains, at the base of the Southern Alps. This area consists of hills and outwash fans of greywacke material. Areas of native forest persist where the topography becomes too steep to farm. Cows for dairy production as well as beef, sheep, and deer are raised here. As on Banks Peninsula, riparian vegetation varies from native forest with full canopy closure to streams bordered with grass or occasional trees. Gorse, blackberry and broom are common.

Field Methods

In-stream measurements: Stream width, depth, substrate size and macrophyte coverage were measured across transects at eight equally-spaced stations along each site reach. Channel shading measurements, and nitrogen and phosphorus samples were taken once at each of the eight stations. Other variables (temperature, travel time, chlorophyll-A and particulate matter) were measured at different points on the site reach. Table 1 gives more detail on each of the methods used.

Riparian zone characterization: I established ten riparian transects along each reach which extended ten metres on either side of the stream. At one metre intervals along each transect I recorded the type of canopy (none, hedge, pine, willow, native plant, deciduous), as well as the height and type of vegetation (bare earth, detritus/leaf litter, ferns, broad leaved plant, grass, tussock, flax, shrubs, brambles) at that point.

Sonde deployment: I measured production and respiration using the open water single station method (Bott 2007). This involved installing a calibrated oxygen sensing data logger (D-Opto Logger, Zebra-tech, Nelson, New Zealand) in the thalweg at the most downstream station of each stream. Sondes were programmed to record oxygen concentration every five minutes and left in each stream between two and five days. To minimize variation in photosynthetic oxygen production due to cloud cover I tried to obtain measurements during at least one day without cloud in each logging period.

Table 1. Methods used to measure in-stream characteristics at each of the 21 stream sites in Canterbury.

In-stream variable	Method
Stream width	Wetted width at eight transects along the stream reach.
Stream depth	Stream depth at ten equidistant points along each of eight stream transects.
Substrate size	We measured the longest side of the pebble or cobble directly beneath ten equidistant points along each of eight transects. Particles too small to measure were classified as sand (0.06-2 mm) or silt (<0.06mm).
Macrophyte coverage	Presence or absence of macrophytes directly beneath ten equidistant points along each of eight stream transects.
Channel shading	We used a densitometer (Lemmon 1956) at ten equally spaced mid channel points along each reach to estimate the percentage channel shaded (Harding et al. 2009). In long reaches where the reach site was not representative of the entire re-aeration reach, we estimated shading using transects across satellite photographs (Google, 2009) of each stream reach.
Nitrogen and phosphorus samples	Filtered (Labserv glass microfibre filter (LBS0GFF.047), Thermofisher Scientific, North Shore City, New Zealand) water samples were taken from the thalweg at each station along stream reaches. These were kept on ice for transporting back to the laboratory, where they were frozen until analysis.
Fine benthic organic matter (FBOM) and fine inorganic sediments	Stove pipe core samples (radius = ten centimetres) were taken at three locations (downstream, mid, upstream stations) along the reach. Sediment down to a depth of ten centimetres was stirred, stream depth recorded, and a one litre sample of the suspended material taken.
Temperature	Probe (D-Opto Logger, Zebra-tech, Nelson, New Zealand)
Travel time and velocity	A known concentration of salt was released above the upstream station. We recorded conductivity (CT2X cableless conductivity level temperature logger, Envco Environmental Equipment Suppliers, Auckland, New Zealand) over time at the downstream station. We measured travel time as the time taken for fifty percent of the salt solution to travel the reach, and velocity as reach length divided by travel time.
Chlorophyll-A	We selected twenty cobbles from throughout the reach at each site for Chlorophyll-A analysis. These were kept on ice for transporting back to the laboratory, where they were frozen.

Propane injection: I measured gas exchange in each reach by propane evasion (Bott 2007). This involved bubbling propane into the top of each stream reach along with a conservative tracer (either rhodamine or sodium chloride) as a continuous addition and collecting water samples at eight stations along the reach once steady state (three times travel time) was reached. These water samples were later analysed for propane and sodium chloride or rhodamine concentration. To sample propane, I took fifty millilitre water samples with a syringe and injected five millilitres of helium into this sample using a three-way stop valve. Samples were shaken for two minutes to facilitate fractionation of propane from water into helium, then propane samples were taken from the syringe headspace, and injected into previously helium flushed and evacuated three milliliter glass vials (Vial type 2, Exetainer, Labco, Buckinghamshire, UK).

Laboratory Methods

Nutrients, particulate matter and chlorophyll-A: Water samples were analyzed for nitrate and phosphate using automated calorometry (EasyChem Plus, Systea Scientific, Anagni, Italy). Nitrate was analyzed by cadmium reduction and soluble reactive phosphate by molybdate reduction (Eaton et al. 1995). Ammonium was measured using the fluorometric method of Holmes and colleages (1999). Particulate matter was dried at 50 ^{o}C for at least 48 hours, weighed, ashed (540 ^{o}C, 4 hours) and re-weighed to find the weight of both organic and inorganic particulate material. The weight of particulate matter was adjusted for water volume to give an estimate per benthic area. Algal chlorophyll-A was extracted from five fist-sized cobbles per site using a method based on Sartory and companions (1984). This involved soaking the cobbles in a known quantity of ethanol,

warming them in a 78 $^{\circ}$C waterbath for 5 minutes, then refrigerating them for 12 to 18 hours before measuring chlorophyll-A concentration with a flourimeter (Trilogy Laboratory Fluorometer, Turner Designs, Sunnyvale, California, US).

Light measurements: Light data were assembled from the national climate database 'CliFlo' which stores data from a network of weather stations across New Zealand (CliFlo 2010). I used daily solar global radiation data (radiation from both direct sunlight and scattered by clouds) from the nearest sampling station to each stream. I also generated a measure of "available light" which was equal to the percentage stream channel not shaded multiplied by daily radiation.

Catchment land-use: To quantify the areas of land-use types within catchments, I used land cover information from the New Zealand land use map (LUMv003, Ministry for the Environment, New Zealand, available from koordinates.com), which is based on satellite imagery taken between 1990 and 2008. This divides land cover into many categories, including forest, woody grassland, high and low production grassland and cropland. Using geographic information systems software (ArcMap version 9.3, ESRI, Redlands, California, United States) I delineated the catchments of each site, and recorded the area of each land-use category within each catchment.

Propane analysis and estimation of re-aeration: Propane samples were analyzed using gas chromatography (Shimadzu GC-2010, with FID detector, Shimadzu Scientific Instruments, Kyoto, Japan; Column: Restek RTX-5Sil-MS, inlet temp 220 $^{\circ}$C with a split of 10:1, column flow was 1.2mL/min, He carrier with control by linear flow; initial temp 50 $^{\circ}$C, rising at 10 $^{\circ}$C/min to 100 $^{\circ}$C, then rising at 100 $^{\circ}$C/min to 200 $^{\circ}$C for 4 min; detector temp: 280 $^{\circ}$C). Where dilution occurred along a reach, I corrected the propane

concentration in proportion to changes in the conservative tracer concentration. The re-aeration rate of propane was calculated from the rate of propane decrease over the reach and converted to that of oxygen by multiplying it by an empirically derived conversion factor of 1.39 (Mulholland et al. 2005). In several streams on the Plains, with a low gradient and correspondingly low re-aeration rate, my reach length was insufficient to detect a statistically significant decrease in propane. For analysis of these streams I used re-aeration values estimated from the night-time regression method (Odum 1956), by plotting rates of oxygen change against the oxygen saturation deficit (in 25 minute bundles to reduce noise) for the time directly after sunset. The slope of this relationship is equal to the re-aeration rate. This method assumes the rate of oxygen concentration change relative to the saturation deficit is only due to re-aeration. Groundwater, rainfall, short upstream reaches, stream gradient and canopy cover prevented reliable estimation of re-aeration by this method in some streams. These streams were discarded from the analysis. All estimates of re-aeration were corrected to a standard temperature before comparisons.

Calculation of metabolism: Oxygen saturation values from each stream were corrected to pressure at mean sea level using barometric pressure data from the nearest weather station (CliFlo 2010). Gross primary productivity and ecosystem respiration for each stream were calculated in five minute intervals by assuming that changes in oxygen concentration ($\Delta O2$) between successive readings were due only to production by photosynthesis (P), consumption by respiration (R), and exchange between water and air (K); i.e., $\Delta O2 = P + R + K$. I calculated respiration over five minute periods from the night-time rate of oxygen change and the re-aeration rate. Because there is no photosynthesis during the night, the rate of oxygen change is the sum of respiration (R) and re-aeration

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(K). I estimated daytime respiration as the average of predawn (midnight-dawn) and post sunset (sunset-midnight) respiration rates, corrected for temperature. I calculated gross primary production (P) from the change in oxygen saturation minus the amount of respiration and re-aeration, for each five minute period; i.e., $P = \Delta O2 - (R+K)$.

Statistical analysis: To identify the important factors influencing metabolism, I regressed each measured riparian, catchment and in-stream variable against primary production, respiration and the P:R ratio. Riparian, catchment or in-stream variables that were not significantly correlated with metabolism were discarded from the analysis. To investigate the relative importance of significant variables, I performed stepwise regressions of each different combination of significant variables. The factors which, when regressed together gave the highest p and r^2 values were interpreted as being the most significant controls on metabolism.

RESULTS

This section starts with a description of the study streams, riparian conditions, organic matter stocks and stream metabolism, then moves on to an account of how catchment land-use influenced stream metabolism, and finally, how riparian factors influenced stream metabolism in relation to my hypotheses.

Stream characteristics: Streams were generally first or second order, two or three metres wide, and cobble-bottomed. Plains streams had greater accumulations of fine inorganic sediment due to erosion from the landscape than did foothills or Peninsula

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streams. Piston velocities of gas exchange (re-aeration x depth) varied, and were correlated with stream slope (p <0.01, $r^2 = 0.47$; Figure 2 & Table 2).
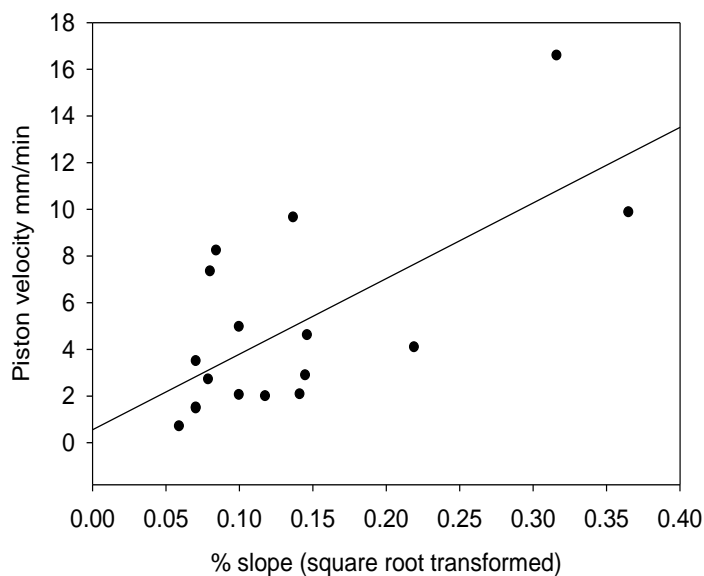

Figure 2. Log piston velocity (reaeration/minute x depth) in relation to stream slope (square-root transformed) in Canterbury streams

There were strong regional patterns in nutrient concentrations. Nitrate concentrations were higher in the Plains region than in the Banks Peninsula or foothill regions. Ammonium was lowest in the foothill region, and phosphate was highest in the Banks Peninsula region (Table 2). Nitrate was positively correlated with catchment area highly productive grass or crop land (p <0.01, $r^2 = 0.64$).

Table 2. General characteristics of the 21 streams we sampled.

Stream Characteristics	Median	Range
Width (m)	2.7	1.1 – 7.6
Depth (m)	0.12	0.07 – 0.37
Velocity (m/min)	4.5	0.02 – 0.29
substrate size (m)	0.043	0.0001 – 0.17
Gradient	2%	0.7% - 13.3%
Fine inorganic sediment (g/m^2)	153	14 - 1840
Plains	170	
Peninsula	72	
Foothills	81	
Piston velocity (mm/min)	2.9	0.7 – 16.6
Nitrate (mg/L)	0.04	0.006 - 7.45
Plains	1.86	
Peninsula	0.03	
Foothills	0.03	
Ammonium (µg/L)	4.70	2.0 – 30.4
Plains	3.60	
Peninsula	6.85	
Foothills	3.20	
Phosphate (µg/L)	13.4	2.2 – 190
Plains	20	
Peninsula	44.4	
Foothills	8.64	

Riparian condition: Out of all the riparian variables, shading had the strongest influence on metabolic rates (judged by the lowest p and highest r^2 values), so I used this to characterize riparian condition. Grass was the most frequently encountered riparian plant, occurring at 18 sites (86%) either under trees or on its own. Gorse was also

common, occurring at 9 sites (43%). Stock had access to 8 of the streams sampled. Average shading over streams ranged from 0-65% for Plains streams, 0-95% for Banks Peninsula streams and from 2-93% in the Foothills.
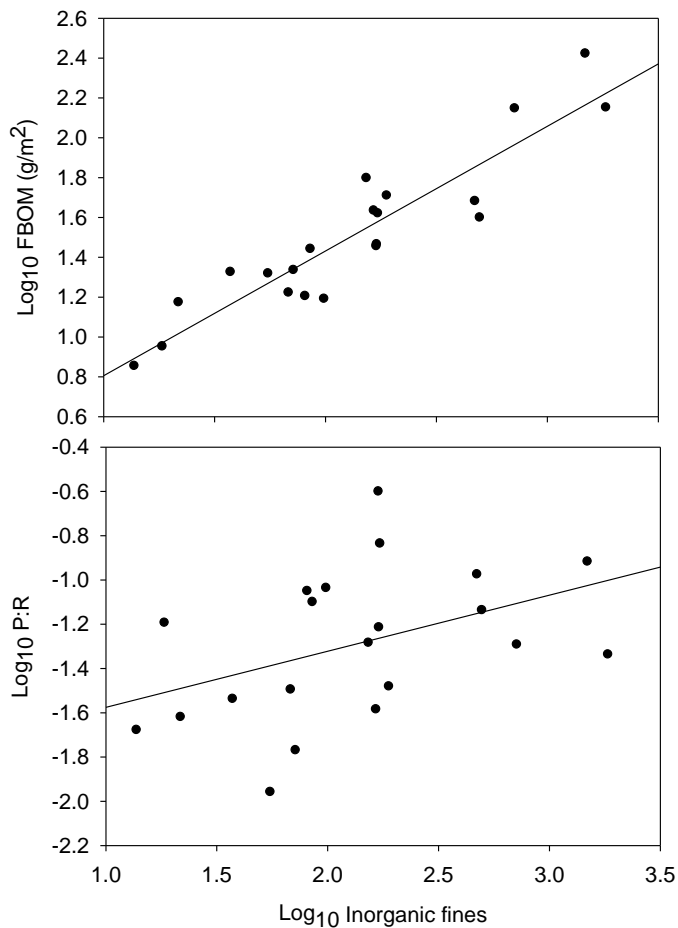

Figure 3. Top: Fine benthic organic matter (FBOM) relative to inorganic fine sediment in my stream sites across Canterbury. Bottom: Production to respiration ratios relative to inorganic fine sediment in each of my stream sites.

Organic matter stocks: Standing stocks of macrophytes were correlated with riparian and land-use variables. Most streams (71%) contained macrophytes, and these covered from 2% to 85% of stream beds. Macrophyte cover was negatively correlated with channel shading (p 0.01, $r^2 = 0.32$), but positively associated with percent catchment area

in highly productive grass or crop land (p <0.01, $r^2 = 0.38$), and with nitrate concentration (p 0.03, $r^2 = 0.24$). However, benthic chlorophyll-A concentrations (median: 17.3 $\mu g/m^2$, range 6.3 - 70.1 $\mu g/m^2$) were not correlated with shading, catchment land-use, water temperature or light (p >0.1, $r^2 = <0.13$ in all cases).

Standing stocks of fine benthic organic matter (FBOM median: 28.58 g/m^2, range: 7.2 - 26.4 g/m^2) were not related to shading, land use or riparian vegetation. The total mass of FBOM was positively correlated with fine inorganic sediments (p <0.01, $r^2 = 0.85$, figure 3). The ratio of FBOM to inorganic sediments was positively correlated with percent channel shade (p 0.04, $r^2 = 0.20$) and riparian canopy cover (p 0.05, $r^2 = 0.19$). The ratio of FBOM to inorganic sediments was also negatively correlated with percent catchment area in highly productive grass or crop land (p 0.01, $r^2 = 0.33$), macrophyte cover (p 0.02, $r^2 = 0.25$) and inorganic sediments (p <0.01, $r^2 = 0.68$).
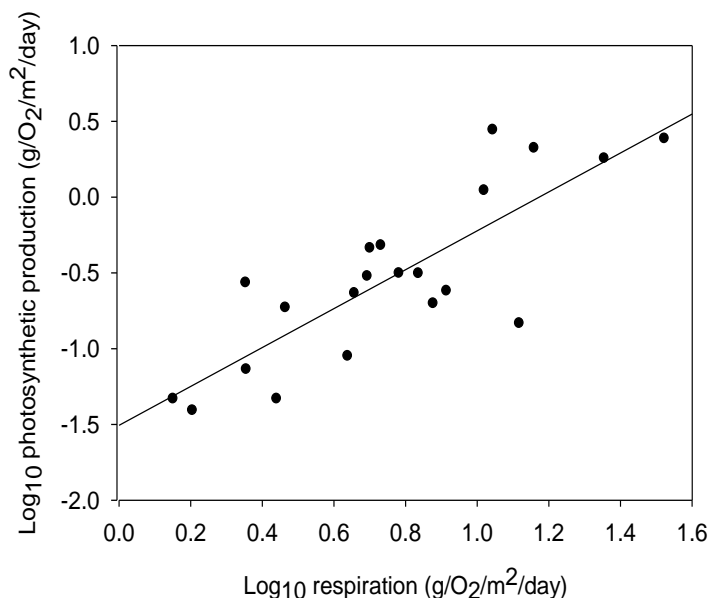

Figure 4. The relationship between production and respiration in 21 Canterbury streams.

Ecosystem metabolism: Gross primary production (P) ranged between 0.04 and 2.78 g O_2 m^2 day^{-1} (median: 0.27 g O_2 m^2 day^{-1}), and respiration (R) between 1.4 and 33.3 g O_2 m^2 day^{-1} (median: 5.39 g O_2 m^2 day^{-1}). P and R were strongly and positively correlated (p <0.01, r^2 = 0.68; Figure 4). All streams were heterotrophic and the production to respiration ratio (P:R) varied from 0.01 to 0.25 (median: 0.05). The increases in P:R were due more to increases in P than to changes in R. Temperature was positively correlated with P (p <0.01, r^2 = 0.42) and P:R ratios (p <0.01, r^2 = 0.49) but, curiously, not with respiration (p 0.11, r^2 = 0.13).
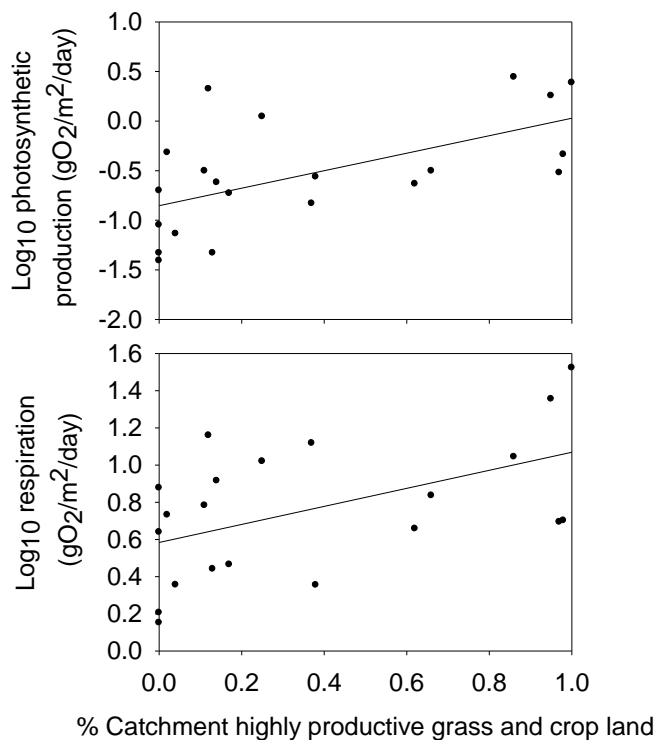

Figure 5. Production and respiration in relation to intensive land-use (high productivity grass and crop land) in streams across Canterbury.

Catchment land-use had a significant effect on stream metabolism. Percent catchment area in high productivity grass or crop land was positively correlated with P:R ratios (p 0.04, $r^2 = 0.20$), P (p <0.01, $r^2 = 0.36$, slope = 0.88) and R (p 0.02, $r^2 = 0.26$, slope = 0.48; Figure 5).

Shading by riparian vegetation suppressed autrotrophic production. As I predicted, shading had a very strong effect on stream P, R and P:R ratios. Shading was closely correlated with P (p <0.01, $r^2 = 0.76$) and R (p <0.01, $r^2 = 0.50$). Variation in P:R ratios was best explained by shading and secondarily by nitrate concentration (p <0.01, $r^2 = 0.63$; Figure 6), as was P (p <0.01, $r^2 = 0.88$). This suggests that trophic state in these streams was primarily regulated by light and riparian shading, and that production was secondarily limited by nitrogen availability.
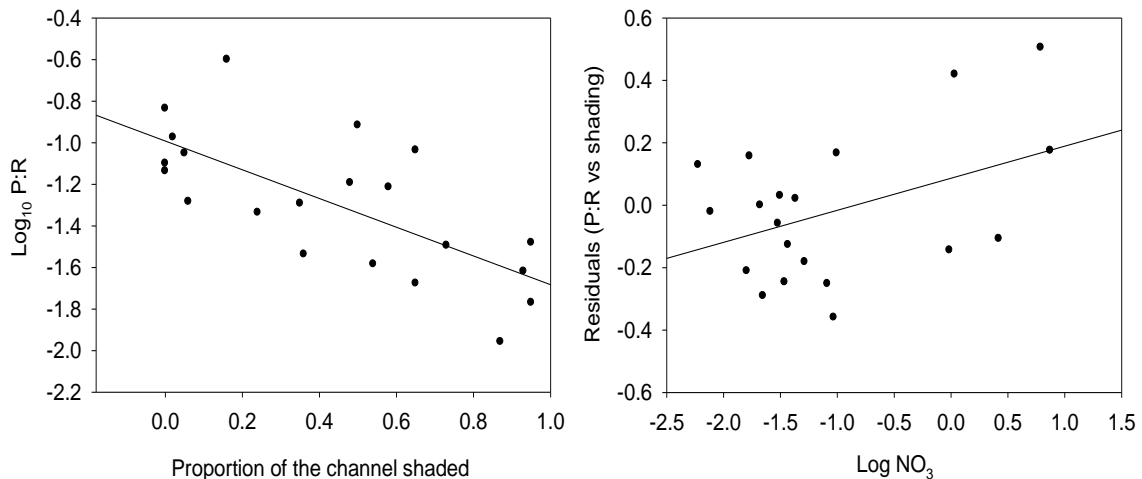

Figure 6. Left: Production to respiration (P:R) ratios relative to the proportion of the stream channel shaded in 21 Canterbury streams. Right: Residuals of the relationship between P:R and shading (left) plotted against stream nitrate concentrations.

Changes in stream trophic state were mainly due to increases in autotrophs, primarily macrophytes. Macrophyte coverage had a positive effect on P (slope = 1.54, p <0.01, r^2 = 0.39), R (slope = 0.89, p 0.01, r^2 = 0.29) and P:R ratios (p 0.03, r^2 = 0.22). Macrophyte coverage, and secondarily chlorophyll-A, best explained P:R (p <0.01, r^2 = 0.50) and P (p 0.00, r^2 = 0.50; Figure 7).
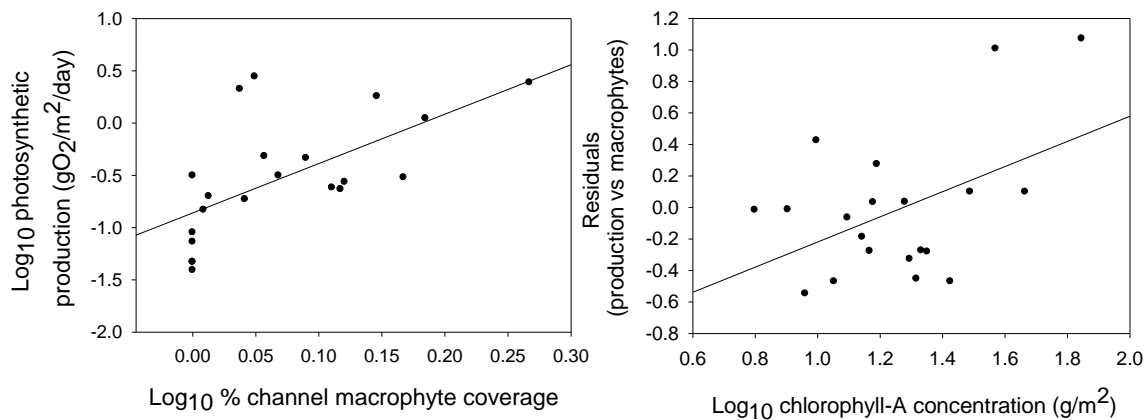
Figure 7. Left: The relationship between primary production and macrophyte coverage in 21 Canterbury streams. Right: Residuals of the relationship between production and macrophyte coverage and stream chlorophyll-A concentrations.

DISCUSSION

Across the 21 streams in this study, I found a strong gradient of trophic states, from oligotrohic to eutrophic. I saw huge increases in primary production and respiration from the forested streams in the Banks Peninsula and foothill regions to the agriculturally-dominated streams of the Canterbury Plains.

Surprisingly, despite the large increases in primary production, all of the streams were net heterotrophic (i.e., P:R ratios were always less than one) as primary production

and heterotrophic respiration increased together across the gradient from oligotrophic to eutrophic. Thus, agriculture contributed towards increases in both primary production and respiration. My results indicate there were two key controls on the extent of eutrophication in these streams: Agricultural land use in the catchments and shading by riparian plants. Below I evaluate these processes and their connections to stream management.

High intensity agricultural land-use increased primary production and respiration rates. Increased production due to high intensity agricultural land use has been widely reported and attributed to increased nutrient supply and decreased canopy cover (Young et al. 1999, Bernot et al. 2006, McTammany et al. 2007, Bernot et al. 2010). However, while respiration is generally sensitive to agriculture, the response of respiration to agriculture has not been consistent. Von Schiller (2008), Bunn (1999) and companions found that respiration increased with agriculture, while Young and Huryn (1999), also working in New Zealand's South Island, found that respiration deceased with agriculture. In my study, contrary to my hypothesis, agricultural streams respired more than the forested streams. Young and Huryn (1999) attributed their results to decreased organic matter inputs in their Otago agricultural streams compared to forested Otago streams. Streams with riparian trees could be expected to have more organic matter inputs, due to falling leaves and woody debris, than open, grassed agricultural streams without trees. However, agricultural streams in my study did not contain less organic matter than forested streams, explaining the difference between our results.

Organic matter entering these open agricultural streams might be grass, effluent, decomposing material associated with soil, or organic matter associated with in-stream

production. The tight positive relationship between organic matter and fine inorganic sediment shows that increases in organic matter were associated with soil erosion. Furthermore, there was no relationship between respiration and quantity of fine inorganic sediment. This is interesting as it suggests that organic matter associated with sediment is not of a type that is readily available for respiration, such as effluent or freshly decomposing material, and instead could be predominantly recalcitrant organic matter associated with eroded soils. Alternatively, the incoming organic material may be available for respiration, but is smothered by inorganic material, so that respiration is less efficient and the oxygenic catabolism of organic compounds less likely, resulting in slower processing rates (Siegrist et al. 1999). Respiration of organic matter buried in fine sediment is also more likely to be anaerobic than organic matter in direct contact with the water column and therefore unaccounted for, as my method of estimating respiration only considers respiration by aerobic organisms. In either case, these findings highlight how different pathways that stressors associated with agriculture (lack of shading and erosion) can interact in a non-additive way. In addition, these results indicate significant regional differences in the impacts of agricultural land use. Reducing stream erosion is likely to decrease respiration in agricultural streams, and this could be one important part of avoiding eutrophication.

Another important part of avoiding eutrophication is reducing in-stream nutrient concentrations. Nitrate is often a limiting nutrient in aquatic ecosystems, and its introduction is commonly associated with increases in production and respiration of organic matter (Dodds 2007, Greenwood et al. 2007). Surprisingly, I found no relationship between respiration and nitrate concentrations. However, nitrate was a secondary factor,

behind shading, in explaining the relative importance of primary production. This is at first surprising because, given the high stream concentrations of NO3- and low concentrations of SRP, I would at first expect phosphorous to be limiting. Phosphorus is a reactive element that tends to associate with sediment, so stream beds may act as a reserve for primary producers. Much of the increase in primary production that I saw was due to rooted macrophytes, which may be able to access phosphorous from fine particulates accumulating beneath the macrophyte beds, enabling them to avoid phosphorus limitation. Clearly, nutrient limitation cannot be inferred from relative stream concentrations, and all pools of available nutrients must be considered in deciding which one is important to manage. Nitrate reduction in these streams is likely to limit primary production.

Changes in primary production were most associated with macrophytes in my study. They correlated more strongly than benthic algae with production and were also most responsive to shading and catchment land-use. Benthic algae were of secondary importance in my study and did not have such a consistent relationship with production, possibly in part due to an inconsistent relationship between chlorophyll-A concentrations and algal productivity (Fellows et al. 2006, Baulch et al. 2009). Previous research by Kaenel and companions (1999) however, found that macrophytes do not always contribute much to stream production, even when they make up a large proportion of the biomass in a stream channel, and stresses the importance of epiphytic algae associated with macrophytes. I did not measure macrophyte-associated or water column algae, so cannot separate their production from that of macrophytes, however it is clear that production associated with macrophytes is a key driver of trophic state change at my sites.

Another key driver of trophic state is temperature. While I found higher production at warmer temperatures, my data showed no strong evidence that water temperature was influencing respiration. Rates of microbial and macrophyte respiration often increase over the temperature range I sampled (Barko et al. 1981, Hill et al. 2000), and temperature has previously been found to be an important control on respiration (Bott et al. 1985). Mulholland (2001) also found no evidence of an effect of temperature on respiration in an inter-biome study of streams in the United States. They suggested that this may be due to the small range of temperatures in their data set compared to the range in nutrients and transient storage. My range of temperatures (7.9 – 17.9 ^{o}C) is also small compared to the range in nutrients (eg nitrate 0.006 - 7.45 mg/L) and organic matter (7.2 - 26.4 g/m^2). Variation in factors that control respiration may also be obscuring the relationship between temperature and respiration in my data set. Evidently, temperature was not a major driver of respiration relative to these factors.

Riparian plants exerted the strongest control on metabolism by shading the stream channel. By influencing both respiration and production, riparian shading was particularly important. The effect of riparian shading on stream metabolism was stronger than either land-use or in-stream characteristics (i.e. standing stocks of organic matter or nutrient concentrations). Shading was associated with decreased rates of both production and respiration, but had a stronger effect on primary production due to light limitation. These findings show that stream eutrophication can be mitigated by riparian shading. My results are supported by previous work showing light limitation overwhelmed larger scale landscape effects on production and respiration (Bunn et al. 1999, Young et al. 1999,

Mulholland et al. 2001, Fellows et al. 2006). In particular, my relationship between shade and metabolism is very similar to that found by Bunn et al (1999) and Fellows et al (2006) in Australian streams, suggesting the relationship is widely applicable across biomes and therefore may be particularly important in managing stream trophic state.

In summary, my study shows that intensive agriculture increases both production and respiration toward eutrophication in streams. Trophic state was primarily controlled by light availability, and secondarily, nitrate concentrations. Inputs of organic matter in open agricultural sites were associated with stream sedimentation and high rates of production and respiration. I found that the effects of agriculture on stream metabolism can be largely overwhelmed by riparian conditions. In order to prevent eutrophication of agricultural streams, I recommend land managers plant and protect riparian zones which reduce stream erosion and increase stream shading.

"We never know the worth of water till the well is dry."

Thomas Fuller

Chapter two: Physico-chemical control of trophic state in Te Wairewa/Lake Forsyth, New Zealand

 ABSTRACT

Te Wairewa/Lake Forysth is a eutrophic, brackish lake in Canterbury, New Zealand, which regularly supports blooms of toxic cyanobacteria, predominatly *Nodularia spumigena*. I examined bloom occurrence in relation to water quality and weather parameters using 17 years of measurements to identify the important factors controlling cyanobacterial blooms in the lake, and to elucidate the role of nitrogen and phosphorus in bloom occurrence. In addition, I performed a series of nutrient addition assays on the lake between December 2010 and February 2011, and measured temperature stratification as an indicator of lake mixing. Short distances of wind travel, shallow lake depths, relatively saline water, decreases in the nitrogen to phosphorus ratio, and massive and rapid increases in nutrients characterized lake blooms. The most likely source of nutrients during large phytoplankton blooms was the lake bed via internal loading mechanisms associated with calm weather. Phytoplankton biomass in mesocosms was primarily limited by nitrogen, a scenario which is likely to increase the competitive advantage of nitrogen fixing cyanobacteria in the lake. My study indicates several potential areas which could be targeted by lake management and deserve further investigation, such as manipulation of lake depth, salinity and sediment binding mechanisms. As the nutrients supporting blooms are primarily being internally sourced, reductions in lake nutrients may be very difficult to achieve, particularly in human timescales.

INTRODUCTION

Eutrophication of aquatic ecosystems is a massive global problem (Smith 2003, Smith et al. 2009). Eutrophication is the process of increasing the amount of energy available for production and/or respiration within an ecosystem, often resulting in weed, algal and cyanobacterial proliferations (Dodds 2006). Within lakes, eutrophication often leads to anoxia in the hypolimnion, the loss of sensitive species and vital ecosystem processes, and the formation of unsightly, often toxic, phytoplankton blooms (Carpenter et al. 1986, Conleyl et al. 1993, Smith et al. 2009). Eutrophication severely reduces the value of water for human consumption, recreation and fisheries (Smith 2003, Smith et al. 2009).

Numerous studies link point and non-point nutrient sources to changes in lake trophic state (Schindler 1971, 1974, Vitousek et al. 1997, Correll 1998, Bennett et al. 2001, Havens et al. 2003, Smith 2003, Lewis et al. 2008, Conley et al. 2009). Nitrogen and phosphorous are considered to be the primary nutrients causing eutrophication within lakes, though which one is generally more important is still debated (Lewis et al. 2008, Conley et al. 2009, Schindler et al. 2009). Fluxes in the cycling of both elements have been massively increased by human population growth and the expansion of agriculture and industry (Vitousek et al. 1997, Canfield et al. 2010). Nutrients other than nitrogen and phosphorus, such as silica and iron, are sometimes also important controls on trophic state in lakes (Beardall et al. 2001, Sterner 2008).

An increased supply of nutrients is not, however, the only factor involved in the overall productivity of lake ecosystems. Macrophyte and phytoplankton growth in lakes can also be limited by local and regional factors, such as light availability (Karlsson et al.

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2009), wind (Ibelings et al. 2007), salinity (Sellner et al. 1988, Blackburn et al. 1996, Musial et al. 2003, Redden et al. 2008), pH (Møgelhøj et al. 2006), temperature (Robarts et al. 1987, Kanoshina et al. 2003), water clarity (Egertson et al. 2004), lake mixing (Berman et al. 1998) and interactions between producers (Møgelhøj et al. 2006) and grazers (Jeppesen et al. 1999, Genkai-Kato 2007).

Te Wairewa/Lake Forsyth is a hyper-eutrophic brackish lake in Canterbury, New Zealand. The lake is of huge cultural significance as well as an important fishery to the local Maori community. In addition, it provides significant habitat for several bird species, such as the rare crested grebe (*Podiceps cristatus australis*), as well as short fin (*Anguilla australis*) and long fin eels (*Anguilla dieffenbachii*). Unfortunately, the lake "blooms" almost annually with large quantities of the toxin producing cyanobacteria *Nodularia spumigena* and in lesser quantity, *Anabaena spp.,* which severely reduce its cultural, resource and recreational value.

Several factors may predispose Te Wairewa to cyanobacterial proliferations, including warm summer temperatures, brackish conditions, a plentiful phosphorus supply, and internal or external mechanisms of nutrient supply which support large blooms. Te Wairewa is very shallow and becomes warm during summer, which is likely to favour the growth of warmth-loving cyanobacterial species such as *Nodularia spumigena,* that have optimum temperatures above 20oC (Huber 1985). The lake's brackish nature may also play an important role in blooms of *Nodularia spumigena*, which can tolerate a remarkable range of salinities, from 0 ppt to more than 20 ppt (Møgelhøj et al. 2006, Myers et al. 2010), but grows best at moderate ranges between approximately 5-20 ppt (Blackburn et al. 1996, Mazur-Marzec et al. 2005, Myers et al. 2010). The brackish

conditions within the lake may favour *N. spumigena* growth and allow it to become dominant over other phytoplankton.

Te Wairewa is located in a catchment that is rich in phosphorus due to the local volcanic geology (Lynn 2005). Weathering, erosion and transport of this rock are likely to have created a large reserve of phosphorus on the lake bed. Phosphorus and nitrogen uptake lengths in two streams draining the Te Wairewa catchment show much stronger demand for nitrogen than for phosphorus, suggesting nitrogen limitation (J. O'Brien, unpublished data). These factors taken together suggest that production within the lake is not likely to be limited by lack of phosphorus, but may be limited by a lack of nitrogen. This environment, rich in phosphorus relative to nitrogen, may also favour cyanobacterial growth over other species of phytoplankton, as many species of cyanobacteria have the ability to fix atmospheric nitrogen, thereby avoiding nitrogen limitation and out-competing other phytoplankton (Schindler 1977, but see Downing et al. 2001).

Although nitrogen fixation may provide an internal source for water column nitrogen associated with cyanobacterial blooms, another possible source of nitrogen to the lake is from the catchment. Fertilizer use, decay of organic matter, septic tanks and leguminous nitrogen fixation within the catchment may contribute to the lake's organic matter budget via transport from the Okuti and Okana streams. Phosphorus from rock weathering, fertilizer, decay or septic tanks may also be entering the lake via catchment streams. Flood events may be particularly important in supplying large amounts of nutrients to the lake.

Alternatively, internal lake mechanisms may mobilize nutrients from the lake bed and satisfy cyanobacterial or algal requirements. Such internal lake mechanisms may

include re-suspension of sediments due to wind mixing, temporary stratification and hypoxia, or increased diffusive flux of nutrients from the sediments. Wind may play an important role in lake blooms by mixing deep water and lake bed sediments rich in nutrients into the water column, effectively fertilizing the water and increasing bloom productivity (Merino-Ibarra et al. 2008). Alternatively, calm days with little wind may allow for short term periods of thermal stratification in the lake. Calm days reduce water column mixing and can allow the formation of low oxygen water layers near the bed of the lake, facilitating phosphorous release from the sediments, as phosphorus is less tightly bound to lake sediments under low oxygen conditions (Correll 1998). Changes in salinity and sulfate concentrations in the lake my also lead to internal eutrophication, a process in which phosphorous diffusion from the sediments increases due to sulfur reduction and binding of ferrous iron (Smolders et al. 2006).

Understanding the mechanisms of nutrient supply to cyanobacterial blooms, and the environmental conditions that favour blooms, will assist Te Wairewa rehabilitation. To add to the current understanding of the blooms, I studied historical bloom occurrence relative to recorded lake chemistry and environmental conditions, and conducted a series of nutrient addition experiments in floating mesocosms in the lake. The aims of the study were: 1) To determine the conditions that characterize periods of high productivity (blooms) in the lake, 2) to examine nutrient limitation of phytoplankton growth and 3) to test which nutrient supply mechanism (external supply of nutrients, internal loading driven by wind or internal loading associated with calm conditions) is responsible for supporting bloom development.

METHODS

Study Area

Te Wairewa is located south of Christchurch on Banks Peninsula, Canterbury, New Zealand (Figure 1). The lake is approximately five kilometers long, one kilometer wide and between one and three metres deep. It is fed by two major tributaries, the Okana and Okuti streams, which merge at the eastern end of the lake. The lake has no natural outlet to the sea but is artificially opened at least once each year to allow fish passage and prevent flooding in the catchment. It usually remains open for only a few weeks as strong ocean currents rapidly build up sediment across the outlet.

Te Wairewa has an interesting geological and human history. The hills surrounding the lake were created by volcanic activity during the formation of Banks Peninsula between 5.8 and 11 million years ago (Hampton et al. 2008). Soils in the catchment reflect this origin, and are particularly high in phosphorus due to rock weathering (Lynn 2005). The lake was once a tidal estuary that became closed off from the sea by a natural build up of sediment across the outlet around 450 years ago (Woodward & Shulmeister 2005). Although inhabited by Maori people, before the arrival of Europeans in the early nineteenth century, much of the catchment was covered in native podocarp-broadleaf forest (Woodward & Shulmeister 2005). This was subsequently almost completely removed for timber, burnt and converted to pasture. This change is reflected in the sediment record of the lake, which shows increased sedimentation and an altered invertebrate assemblage around this time (Woodward et al. 2005). Very little original forest remains, but in stream gullies some native species are regenerating alongside exotics such as grass and gorse (Harding et al. 2006). Land surrounding the lake

is now mainly used for low intensity agriculture, such as sheep farming. There is also

small amount of pine plantation forestry and two small settlements; Little River and

Birdlings Flat.
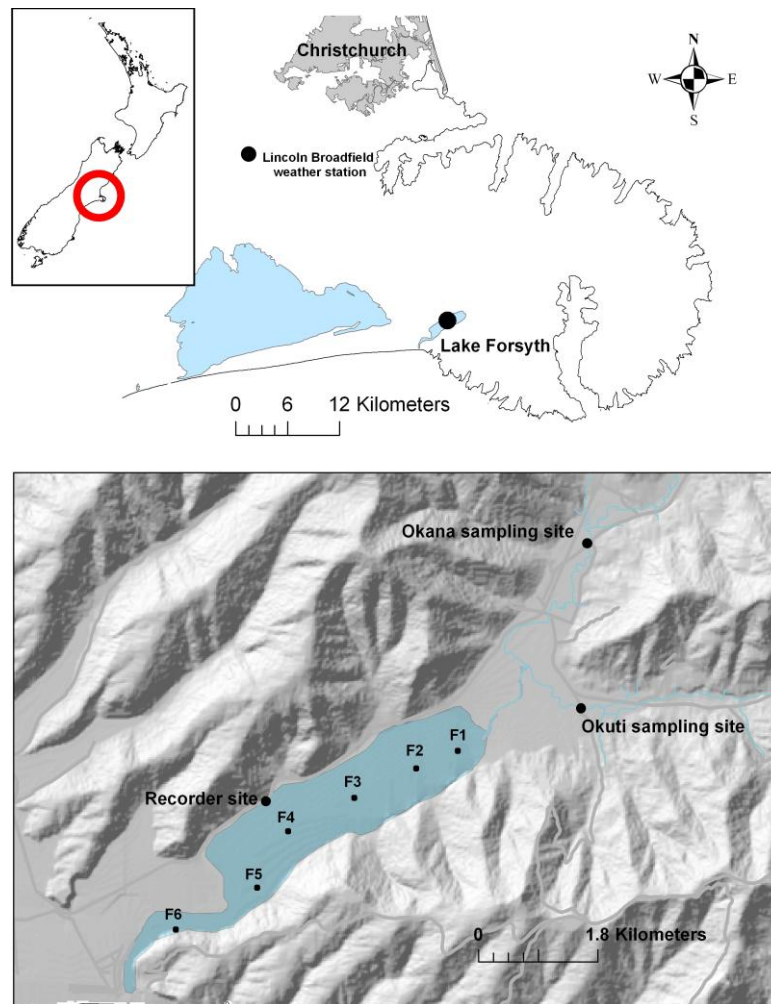
Figure 1. The Te Wairewa/Lake Forsyth study area, located on the south west of Banks Peninsula, Canterbury, New Zealand. Weather data were sourced from the Lincoln Broadfield weather station (top), and lake water quality was sampled at the recorder site and the Okuti and Okana streams between 1993 and 2010. Sites F1, F4 and F6 were used for nutrient limitation experiments and sites F1-F6 for measurement of temperature stratification over the summer of 2010-2011.

Field and laboratory methods

This study used data from three sources. First, water quality data were obtained from the Canterbury Regional Council (Environment Canterbury), who routinely sample a variety of chemical and physical parameters at the lake and the Okana and Okuti streams as part of their surface water monitoring program. This dataset covers seventeen years, from 1993 to 2010. Secondly, weather data came from the national climate database "CliFlo", which stores data from weather stations across New Zealand (CliFlo 2010). Finally, temperature stratification and nutrient addition data came from a series of experiments on the lake that I undertook between December 2010 and February 2011.

Water quality sampling: Lake water quality was sampled by Environment Canterbury staff at a site on the northern edge of the lake next to state highway 75 (called the 'recorder' site, Figure 1). Samples were taken either from the steep rocky embankment

Figure 2. The "recorder site" on the northern shore of Te Wairewa. Source: http://ecan.govt.nz accessed 26.8.11.

bordering the lake or a jetty which extends to a staff gage and recording station (Figure 2). The Okana Stream was sampled where it intersects state highway 75, at the edge of the small township of Little River. The Okuti Stream was sampled where it intersects with Kinloch Road (Figure 1). Sampling was undertaken at weekly

intervals in the lake and monthly intervals in the catchment streams. Parameters sampled

include water temperature, conductivity, salinity, pH, ammonia, nitrate + nitrite nitrogen,

total nitrogen, dissolved reactive phosphorus, total phosphorus, dissolved oxygen, depth,

turbidity and chlorophyll-A. These were sampled according to national protocols for state

of the environment in New Zealand (Ministry for the Environment 2007) and generally

analysed according to methods used by the American Public Health Association (Table 1).

Table 1. A summary of sampling methods used by the Canterbury regional council (Environment Canterbury) to sample water quality at Te Wairewa and in the catchment streams between 1993 and 2010.

Parameter	Unit	Method	Reference
Water temperature	^{o}C	Glass thermometer or temperature probe	
Conductivity	µS/m @ 25 C	Hand held probe	American public health association (APHA) 2510 B
Salinity	ppt	Hand held probe	
Ammonia nitrogen	mg/L	Phenate method	APHA 4500-NH3N F
Nitrate + nitrite nitrogen	mg/L	Cadmium reduction method	APHA 4500-NO3F
Total nitrogen	mg/L	Kjeldahl method	APHA 4500-N C
Dissolved reactive phosphorus	mg/L	Ascorbic acid method	APHA 4500 P B F (autoanalyser)
Total phosphorus	mg/L	Persulfate Digestion,h subsequent analysis on spectrophotometer, using ascorbic acid method	APHA 4500 P B
Dissolved oxygen saturation	%	Dissolved oxygen meter	
Depth	m	Read from staff gauge	
Turbidity	NTU	Lab measurement	APHA 2130 B
Water column chlorophyll-A	µg/L	Flourimetric method (measured between March 1995 – 26 Aug 1999)	APHA 10200
Plankton chlorophyll-A	µg/L	Flourimetric method (measured instead of water column chlorophyll-A between 1 Sept 1999 – 5 Aug 2010)	APHA 10200

Weather: Weather conditions were sampled at the Lincoln Broadfield electronic weather station (Figure 1). I chose this station as it was nearest the lake and contained the most comprehensive records between 1993 and 2010. Twenty four hour wind, rain, air temperature and light sampling data were used (Table 2).

Table 2. Weather variables recorded at the Lincoln Broadfield weather station. Data from this weather station were sourced from the national climate database "CliFlo" (CliFlo 2010).

Parameter	Unit	Method
Wind run (wind travel)	km	Anemometer Distance traveled in 24 hours
Maximum gust	m/s	Anemometer Maximum gust in a 24 hour time period
Wind direction	Degrees true	Wind vane
Rain	mm	Rain gauge
Daily global radiation	MJ	Pyranometer

Temperature stratification: To investigate temperature stratification within Te Wairewa, I established six sites across the lake in early December 2010 (Figure 1, F1 – F6), each with data logging temperature probes (HOBO pendent temperature/light data logger, Scott Technical Equipment, Christchurch, New Zealand) installed at approximately 0.5 m intervals between anchor and buoy.

Nutrient addition: At three sites across the lake (F1, F4, F6) I carried out a series of nutrient addition experiments in mesocosms to investigate nutrient limitation within the lake. This involved putting three liters of lake water (drawn from 0.5m below the water surface using a bilge pump) into each of twelve 3.8 litre "cubitainers" (Cubitainer®, US Plastic Corporation, Lima, Ohio, USA). Pre-prepared treatments of nitrogen (+N), phosphorus (+P) and nitrogen and phosphorus (+NP) were added to nine of these (three replicates of each treatment at each site) while the remaining three were used as controls. The +N treatment consisted of 12µM inorganic N as NO3-, while the +P treatment was 3µM inorganic P as PO4-3 and +NP was both together. Due to the strong winds and waves the lake sometimes experiences, cubitainer lids could not be left off to allow diffusion of air into the mesocosm. However, I made sure the space remaining in each cubitainer (0.8L) was as full as possible with air to reduce carbon limitation effects.

After three or four days on the lake, cubitainers were brought back to the laboratory. Two hundred millilitre samples of water from each cubitainer were filtered (LBS0GFF.047, Labserv glass microfibre filter, ThermoFisher Scientific, North Shore, New Zealand), and chlorophyll-A extracted from the filtrate by extraction with ethanol, using a method based on that of Sartory and colleages (1984). Chlorophyll-A concentrations were measured by flourimetry (Trilogy Laboratory Fluorometer, Turner Designs, Sunnyvale, California, US). I intended to repeat these tests during the summer so that our experiments would be performed over the course of a phytoplankton bloom event. Due to a late and small bloom event, and a serious earthquake this was not possible; however I repeated the assay on four occasions between December and February 2011.

At each of these visits to the lake, I measured pH, temperature and conductivity profiles at sites F1, F4, and F6. In addition, to further understand production and oxygen concentrations in the lake, I measured diel oxygen at these sites over four days in both January and February 2011, using a data logging oxygen probe (D-Opto Logger, Zebra-tech, Nelson, New Zealand).

Data analysis: Occurrence of blooms in relation to lake water quality and weather parameters between 1993 and 2010. I used chlorophyll-A data as my index of phytoplankton abundance. Phytoplankton "bloom" chlorophyll-A levels were initially identified by matching comments about blooms written by Environment Canterbury staff with the chlorophyll data. We classified a "bloom" as chlorophyll measurements above the 75th percentile. This generally matched observer comments about bloom presence or absence in the data. To utilize weather data, I generated averages of weather parameters for the seven day period before each water quality sampling date.

All water quality and weather data were sorted into "bloom", "pre-bloom", and "non-bloom" categories. Pre-bloom data were defined as the sample directly before a "bloom" sample. Because the lake was sampled weekly, in lake samples "pre-bloom" data represents measurements from the week prior to a bloom. However, catchment data were sampled monthly, so "pre-bloom" data here represent samples taken a month before a bloom. To reduce the effect of seasonal variation, I divided bloom, pre-bloom and non-bloom categories into summer and winter categories; "summer" was 15 November to 15 May, whereas "winter" was 16 May to the 14 November. This definition was also designed to separate *Nodularia spumigena* blooms (which generally occur during summer

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and autumn) from smaller proliferations of other cyanobacteria (including picocyanobacteria and *Merismopedia*) which occur during winter. In addition, natural within-season variation in light and temperature may obscure differences in bloom, non-bloom and pre-bloom data means. To address this, I generated averages of light and temperature data over two week intervals, and compared bloom, non-bloom and pre-bloom data, matched by date, to these. Differences in mean bloom, non-bloom and pre-bloom data were initially tested using students T-tests, in order to filter insignificant factors from potentially significant factors. Paired T-tests were used to compare data matched by date. When probability values exceeded 0.1, I concluded there were no significant differences between populations and discarded this factor from further analysis. In order to decrease the risk of a type 1 error, I performed post-hoc Bonferroni corrections for multiple tests on the remaining pool of factors associated with bloom occurence.

Data analysis: nutrient addition assay. I used a repeated measures ANOVA model to analyze the effects of nutrient addition on mesocosm chlorophyll-A concentrations. This involved nesting treatment effects (+N, +P, +NP, C) inside site (F1, F4, F6), which was nested inside the four dates of the assay, and partitioning the variance between treatment effects, site and the assay dates using a generalized linear model. Fisher's least significant difference (LSD) tests were used to compare means.

RESULTS

General lake characteristics between 1993 and 2010

Lake depth, conductivity, salinity, temperature and turbidity at the recorder site varied extremely widely over the years sampled. Depth, temperature and salinity all varied seasonally. The lake was generally deepest, coldest, and least saline in winter and shallow, warm, and saline in summer (Figure 3). Dissolved oxygen saturations varied between the extremes of 51% and 191%, indicating high productivity and highly dynamic conditions.

Lake nutrients: Lake nitrogen and phosphorus concentrations were generally very high and enormously variable. For example, nitrate + nitrite nitrogen ranged two hundred fold from <0.005 mg/L to a maximum of 1.1 mg/L. Likewise, dissolved reactive phosphorus varied between <0.001 and 4.2 mg/L (Table 3).

Weather conditions: Air temperature varied seasonally between the extremes of - 9.5 ^{o}C and 35 ^{o}C. Wind direction and travel varied, but the prevailing wind came from the North East and days without wind (minimum wind run 40 km) were rare. Daily rainfall was low (median = 0 mm), and varied between 0 mm and 73.6 mm (Table 3).

Phytoplankton abundance: Median water column chlorophyll-A (measured between March 1995 and August 1999) was 42.3 µg/L and varied between a minimum of 1.8 µg/L and a maximum of 20300 µg/L. Values above or equal to the 75th percentile (76 µg/L) were classified as "bloom" values. Plankton chlorophyll-A (measured instead of water column chlorophyll-A between September 1999 – August 2010) (median = 28.3 µg/L) ranged between <0.2 µg/L and 1181 µg/L. Values above or equal to the 75th percentile value of 47 µg/L were classified as a bloom. The lake bloomed most dramatically during the summer months of January, February and March (Figure 3).
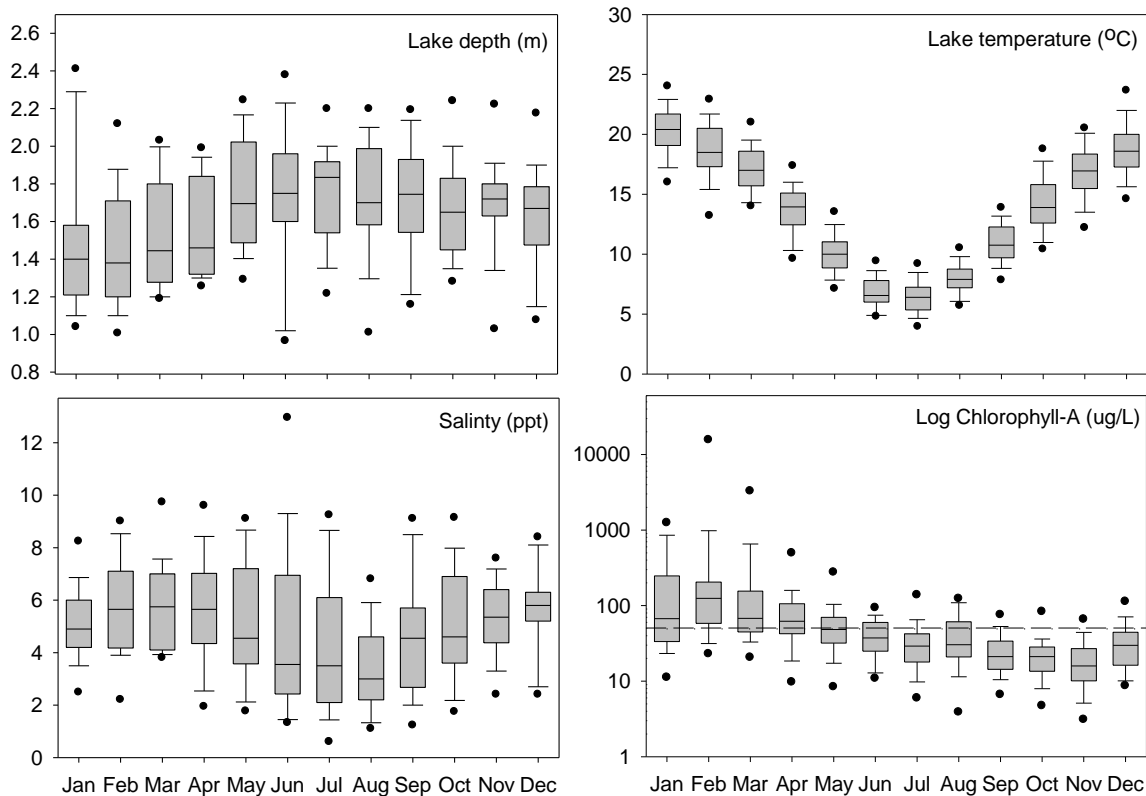
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Figure 3. Annual trends in depth, temperature, salinity and chlorophyll-A in Te Wairewa, Canterbury, New Zealand. Dots represent 5th and 95th percentiles, error bars represent the standard error, and solid rectangles cover 25th to 75th percentiles and are bisected by the median. Dashed line on the chlorophyll graph (bottom right) indicates the planktonic chlorophyll-A concentration at and above which I have defined "bloom" conditions. Data from 17 years (1993 – 2010) of water quality monitoring at the "recorder" site by the Canterbury regional council (Environment Canterbury).

Table 3. Summary statistics for Te Wairewa and Te Wairewa catchment streams between 1993 and 2010. Units are given at first mention.

Lake, weather & catchment	Median	Minimum	Maximum
Lake characteristics			
Depth (m)	1.68	<0.8	2.7
Temperature (^{o}C)	13.2	2.4	25.1
Salinity (ppt)	5	0.3	14.3
Conductivity (mS/m)	920	62	3600
Turbidity (NTU)	14	1.1	1500
Dissolved oxygen saturation (%)	99.8	51	191
Ammonia nitrogen (mg/L)	0.019	<0.005	2
Nitrate + nitrite nitrogen (mg/L)	0.032	<0.005	1.1
Total nitrogen (mg/L)	1.3	0.12	200
Total phosphorus (mg/L)	0.15	<0.008	18
Dissolved reactive phosphorus (mg/L)	0.005	<0.001	4.2
N:P ratio	20.3	3.5	194.6
Weather characteristics			
Median daily global radiation (MJ)	11.91	0.49	35.2
Air temperature (^{o}C)	11.5	-9.3	35
Maximum daily wind gust (m/s)	11.8	2.6	30.9
Median wind run (km)	340	40	1318
Daily rain (mm)	0	0	73.6
Okuti Stream characteristics			
Turbidity	2.75	1.3	15
Ammonia nitrogen	0.018	0.005	0.110
Nitrate + nitrite nitrogen	0.09	0.01	0.54
Total nitrogen	0.23	0.08	0.84
Dissolved reactive phosphorus	0.024	0.010	0.064
Total phosphorus	0.048	0.021	0.580
N:P ratio	10.1	0.6	56.1
Okana Stream characteristics			
Turbidity	2.85	1.4	23
Ammonia nitrogen	0.014	0.005	0.110
Nitrate + nitrite nitrogen	0.110	0.006	1.2
Total nitrogen	0.29	0.08	1.3
Dissolved reactive phosphorus	0.022	0.007	0.068
Total phosphorus	0.045	0.02	0.190
N:P ratio	12.7	1.7	58.2

General lake characteristics between December 2010 – February 2011.

Figure 4. Extensive macrophyte beds at the eastern end of Te Wairewa, Canterbury, New Zealand. Photographed in late January, 2011.

The lake had a strong gradient of conditions along its length. Conductivity increased from the eastern end (median conductivity at site F1: 269 μS cm^{-1}) to the western end nearer the sea (median conductivity at site F6: 2203 μS cm^{-1}). Macrophytes were plentiful from midway between F2 and F3 east (Figure 4) while the western end lacked macrophytes and was visibly more turbid. Diel oxygen patterns differed between sites. F1 showed the most extreme variation in oxygen saturation, from <50 % to >200 %, indicating very high photosynthetic rates. Sites F4 and F6 varied between 80 % to >100 % and <80 % – 120 %, respectively. Water pH differed similarly between sites. Median daytime pH at site F1 was very high at 9.6, while it was 8.4 and 8.7 at F4 and F6, respectively.

Sites showed weak temperature stratification (0 – 6 ^{o}C difference between water at the surface and on the bottom) which generally occurred between late morning and early evening. The frequency of stratification >2 ^{o}C varied between sites sampled. Site F5 stratified rarely while F2 stratified most often (percent days with stratification >2 ^{o}C: F1 = 30%, F2 = 64%, F3 = 53 %, F4 = 48%, F5 = 13 %, and F6 = 56%). This may have been influenced by the relative depth of sites (Median depth F1 = 0.65 m, F2 = 1.2 m, F3 = 1.6

m, F4 = 1.7 m, F5 = 1.7 m, F6 = 2.2 m) localized wind or saline layers within the lake (halo-stratification). However, we did not find evidence of halo-stratification in any site profile of conductivity.

Conditions characterizing lake blooms

Temperature: Overall, mean lake temperature during blooms was significantly higher than during non-bloom periods (bloom: 14.8 $^{\circ}$C, non-bloom: 12.3 $^{\circ}$C, Figure 5, Table 4). Large blooms of *Nodularia spumigena* and *Anabaena sp.* were restricted to summer and autumn months; however, warmer than usual temperatures were not associated with blooms. There was no significant difference in temperature between summer bloom and non-bloom periods or winter bloom and non-bloom periods, and when I compared lake temperature during blooms to non-bloom periods within the same two weeks of each season, I found no differences. Similarly, air temperatures were higher during bloom periods than non-bloom periods when all seasons were combined (bloom mean: 13.1 $^{\circ}$C, non-bloom mean: 10.8 $^{\circ}$C, Table 4), but there were no differences between bloom and non-bloom temperatures when paired within two week intervals. Pre-bloom mean water temperatures were not significantly different from bloom water temperatures, either in summer or winter.

Light: Bloom occurrence was not associated with variations in light. There was no difference between pre-bloom, bloom and non-bloom solar radiation when all seasons were considered together or when pre-bloom, bloom and non-bloom data were compared inside two week intervals (Table 4).

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Wind: Phytoplankton blooms in both summer and winter were associated with calm weather. Median wind run was shorter during bloom periods than non-bloom periods (summer bloom: 360 km, summer non-bloom: 396 km, Figure 5; winter bloom: 298 km, winter non-bloom: 340 km, Table 4). Pre-bloom and non-bloom wind run were not significantly different and blooms were not associated with any particular wind direction.

Lake turbidity: Blooms were associated with increased lake turbidity because of increased phytoplankton biomass, but not because of increased suspended sediments. Turbidity during blooms was much higher than during non-bloom periods (bloom mean: 61 NTU, non-bloom mean: 19 NTU, Table 4), but bloom turbidity to chlorophyll-A ratios were not different to non-bloom turbidity to chlorophyll-A ratios. There was no difference between pre-bloom and non-bloom turbidity and turbidity to chlorophyll-A ratios.

Catchment turbidity: There was no evidence from catchment turbidity and rainfall data that catchment floods were associated with blooms. In fact, mean turbidity was lower during bloom periods than during non-bloom periods in both the Okana and Okuti streams (Okana bloom: 2.39 NTU, non-bloom: 4.83 NTU; Okuti bloom: 2.57 NTU, non-bloom: 4.01 NTU, Table 4). Mean rainfall during blooms was not significantly different to non-bloom rainfall. Pre-bloom turbidity and rainfall were also not different from non-bloom turbidity and rainfall.

Depth: Interestingly, the lake was significantly shallower during bloom periods than during non-bloom periods (bloom: 1.50 m, non bloom: 1.74 m, Figure 5). When I compared data within seasons, mean lake depth during summer blooms was shallower than during non-bloom periods (summer bloom: 1.45 m, non-bloom: 1.74, Table 4), but

there was no significant difference between winter bloom and non-bloom depths. Pre-bloom depths did not significantly differ from non-bloom depths.
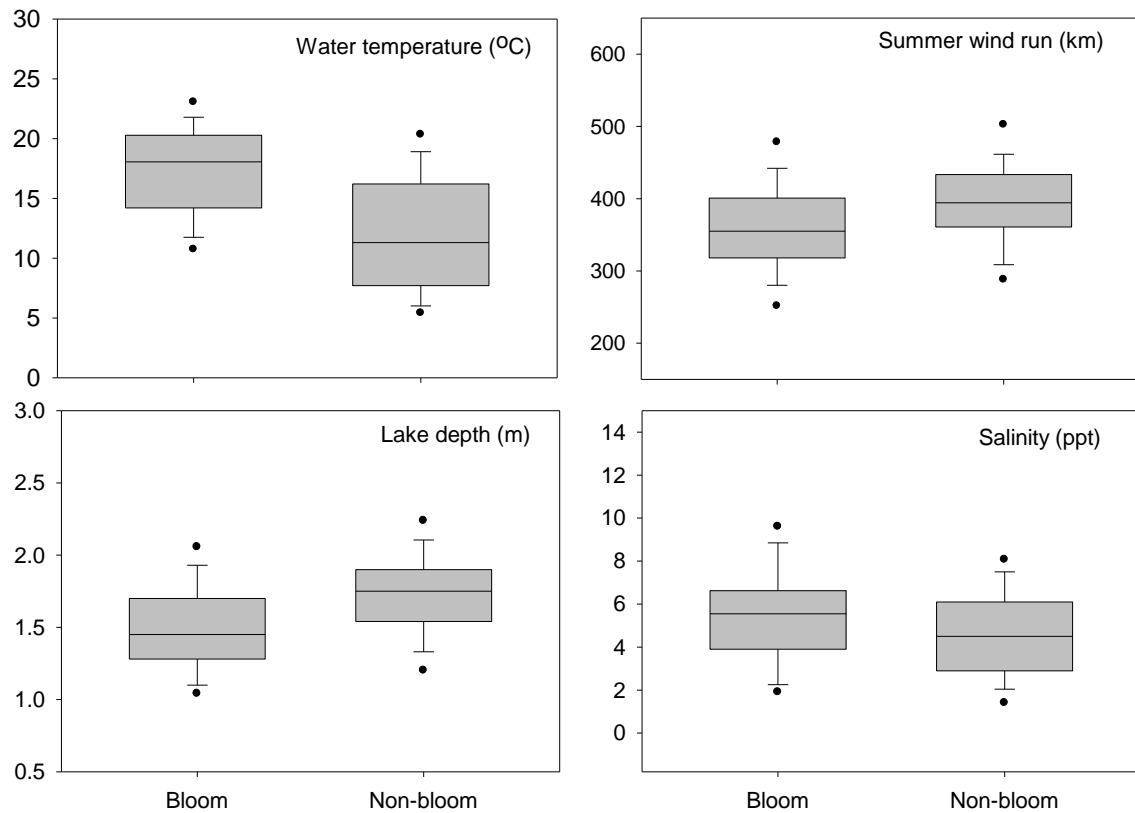

Figure 5. Temperature, depth, wind run and salinity in relation to cyanobacterial bloom occurrence in Te Wairewa, Canterbury, New Zealand, between 1993 and 2010. All comparisons in this figure are significantly different with Bonferroni corrected probabilities of less than 0.01 from T-tests.

Salinity: Mean salinity during blooms was higher than that during non bloom periods (bloom mean: 5.3 ppt, non-bloom mean: 4.7 ppt, table 4, Figure 5). There was no significant difference between pre-bloom and non-bloom salinity.

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Lake nutrients: Lake nutrient concentrations were generally much higher during blooms than during non-bloom periods. Total nitrogen during blooms was almost five times that of non-bloom periods (mean bloom: 5.82 mg/L, non-bloom: 1.24 mg/L) and total phosphorus concentrations also showed large increases during bloom periods (mean bloom: 0.63 mg/L, non bloom: 0.15 mg/L). Mean bloom molar N:P ratios were lower than non bloom N:P ratios (bloom: 20.2 , non-bloom: 26.4).   There was no difference between pre-bloom and non-bloom average nutrient concentrations or N:P ratios (Table 4 and Figure 6).

Table 4. A summary of mean physico-chemical characteristics during lake cyanobacterial blooms compared to periods without blooms. Probability values shown have been Bonferroni corrected.

Parameter	Mean bloom	Mean non-bloom	T value	df	p value
Lake characteristics					
Temperature (oC)	14.8	12.3	6.011	436.06	<0.01
summer	17.1	16.4	1.872	294.77	ns
winter	9.0	10.1	-2.405	115.79	ns
Turbidity (NTU)	61	19	4.216	172.45	<0.01
Turbidity/chlorophyll-A	1.553	0.836	0.607	165.60	ns
Depth (m)	1.50	1.74	-8.352	377.21	<0.01
summer	1.45	1.74	-6.167	166.54	<0.01
winter	1.61	1.75	-2.531	74.193	ns
Salinity (ppt)	5.3	4.7	4.260	426.09	<0.01
summer	5.6	5.3	1.244	230.54	ns
winter	5.3	4.4	2.599	95.611	ns
Ammonia (mg/L)	0.087	0.046	2.103	265.66	ns
Nitrate + nitrite (mg/L)	0.049	0.072	-2.395	445.51	ns
Total nitrogen (mg/L)	5.82	1.24	2.845	156.23	0.06
Dissolved reactive phosphorus	0.070	0.008	2.300	159.40	ns
Total phosphorus (mg/L)	0.63	0.15	3.399	159.99	<0.01
N:P	20.2	26.4	-4.039	438.51	<0.01

Parameter	Mean	Mean	T value	df	p value
Weather characteristics					
Air temperature (oC)	13.1	10.8	4.976	194.45	<0.01
Daily global radiation (MJ)	13.24	14.28	-1.487	370.14	ns
Median daily wind run (km)	344	358	-1.942	326.71	ns
Summer	360	396	-4.027	193.97	<0.01
Winter	298	340	-3.528	62.229	<0.01
Rainfall (mm)	1.69	1.69	-0.018	304.33	ns
Okana Stream characteristics					
Turbidity	2.39	4.83	-3.002	34.552	0.06
Ammonia	0.017	0.018	-0.311	156.07	ns
Nitrate + nitrite	0.10	0.24	-4.259	153.23	<0.01
Total nitrogen	0.26	0.42	-3.650	135.81	<0.01
Dissolved reactive phosphorus	0.028	0.021	4.573	108.51	<0.01
Total phosphorus	0.059	0.046	2.818	86.425	0.07
N:P	13.2	21.2	-3.819	104.38	<0.01
Okuti Stream characteristics					
Turbidity	2.57	4.01	-2.752	36.111	0.10
Ammonia	0.021	0.019	1.010	111.45	ns
Nitrate + nitrite	0.09	0.15	-3.885	155.42	<0.01
Total nitrogen	0.21	0.29	-3.513	139.03	<0.01
Dissolved reactive phosphorus	0.029	0.024	3.408	109.64	0.01
Total phosphorus	0.064	0.047	1.846	63.384	ns
N:P	9.8	15.6	-4.536	131.93	<0.01

Catchment nutrients: Surprisingly, catchment concentrations of nutrients during blooms were different from non-bloom concentrations. Mean bloom nitrogen to phosphorus ratios (N:P), nitrate + nitrite nitrogen concentrations, and total nitrogen concentrations, were lower than non-bloom concentrations in both streams. Mean bloom concentrations of dissolved reactive phosphorus were higher than non-bloom dissolved reactive phosphorus in both streams, and bloom total phosphorus concentrations were higher in the Okana, but not the Okuti (Table 4 & Figure 6).
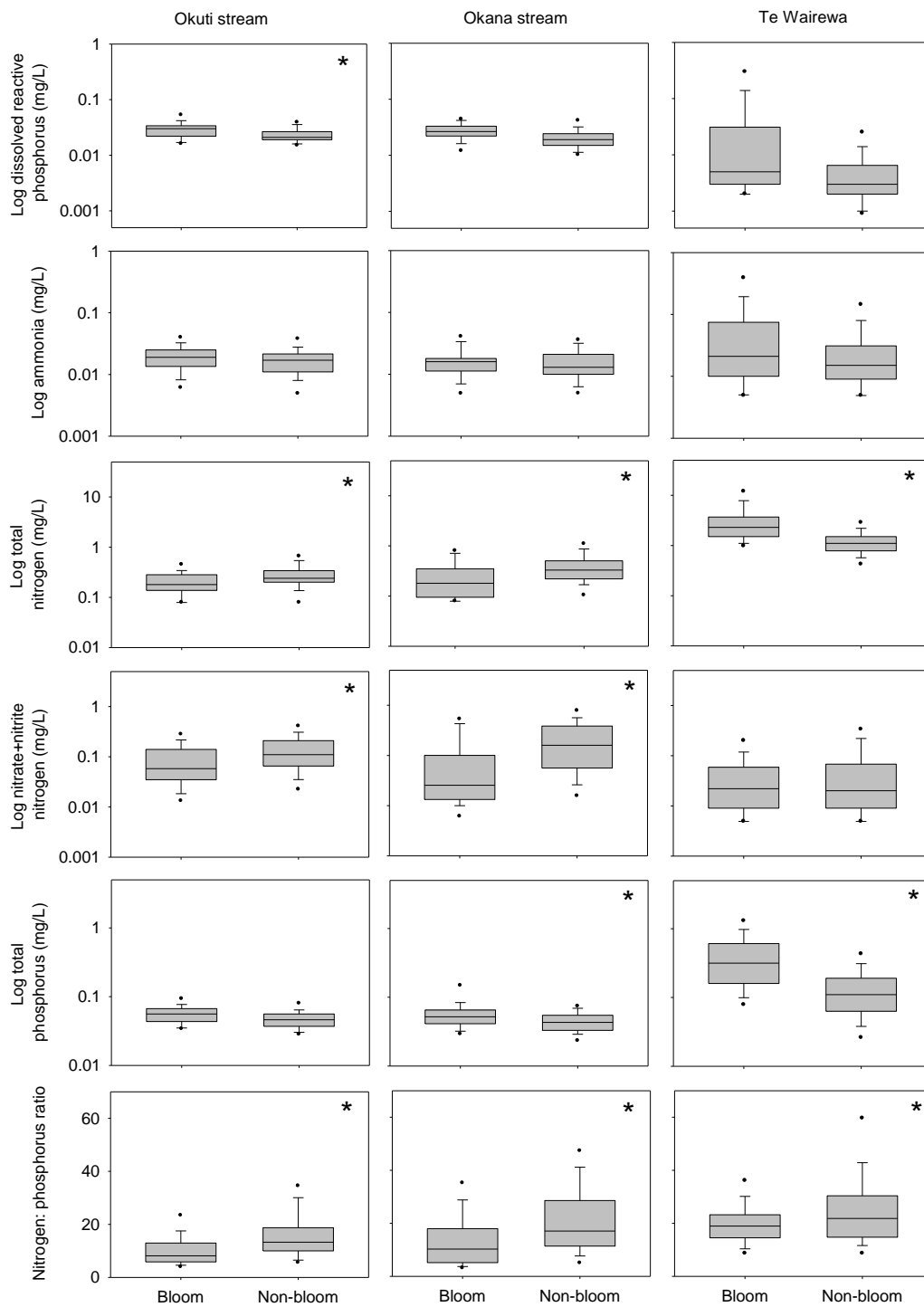
52

Figure 6.   Nutrient concentrations relative to bloom occurrence in Te Wairewa, Canterbury, New Zealand, between 1993 and 2010.   Log is to base 10, the symbol * denotes probability values of less than 0.01.

Nutrient limitation of phytoplankton growth

Nitrogen addition consistently increased phytoplankton abundance within the experimental mesocosms, but phosphorus addition did not have an effect, except at one site. This was shown in the significant main effect of nitrogen addition on chlorophyll-A concentration, the lack of an independent phosphorus effect, and the significant effect of nitrogen, phosphorus and site (Table 5, Figure 7 and 8).

Table 5. Repeated measures generalised linear model table for mean chloroplyll-A concentration in nutrient addition mesocosms. Nutrient addition experiments were carried out at three sites on Lake Forsyth, on four occasions between December 2010 and February 2011.

| Source	df	MS	F	P
Between subjects				
Nitrogen	1	2607.36	11.45	0.003
Phosphorus	1	0.02	0.000	0.992
Site	2	3483.26	15.30	<0.001
Nitrogen × phosphorus	1	0.63	0.003	0.959
Nitrogen × site	2	187.43	0.823	0.452
Phosphorus × site	2	38.42	0.167	0.846
Nitrogen × phosphorus ×	2	779.24	3.422	0.050
Error	23	227.71		
Within subjects				
Date	3	2459.31	12.81	<0.001
Date × nitrogen	3	6.96	0.036	0.991
Date × phosphorus	3	36.62	0.191	0.902
Date × site	6	2979.71	15.52	<0.001
Date × nitrogen ×	3	284.64	1.482	0.227
Date × nitrogen × site	6	60.66	0.316	0.927
Date × phosphorus × site	6	98.69	0.514	0.796
Date × site × nitrogen ×	6	347.27	1.809	0.110
Error	69	192.00		
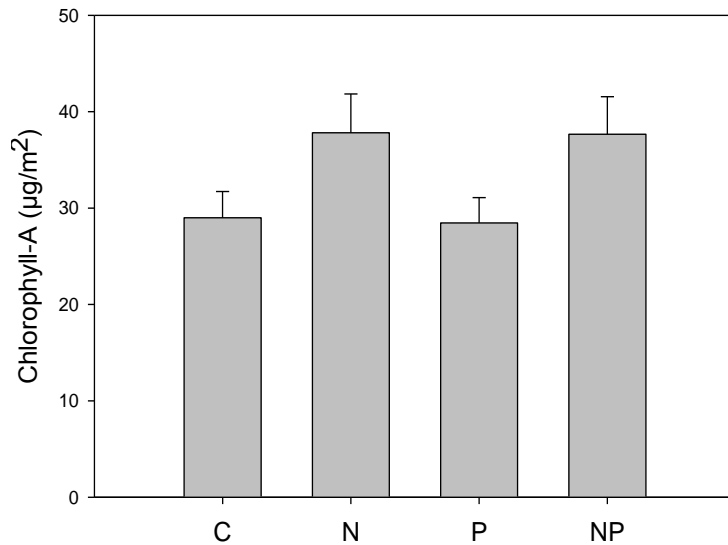
Figure 7. Mean (+SE) chlorophyll-A concentration relative to the nutrient added (C: Control; N: Nitrogen; P: Phosphorus; NP: Nitrogen and phosphorus) in nutrient addition mesocosms at Te Wairewa. This graph shows treatment effect across all sites combined.

Nitrogen and phosphorus addition increased phytoplankton abundance at site F1, but did not at sites F4 or F6. I found a significant effect of date on chlorophyll-A concentration, which shows that phytoplankton abundance changed through time. Additionally, there was a significant effect of date and site on chlorophyll-A concentration, which indicates that some sites had bigger changes through time than other sites. However, there were no date interactions nitrogen and phosphorus, which shows that the effects of nitrogen and phosphorus addition at each site were consistent over time (Table 5, Figure 8 and 9).
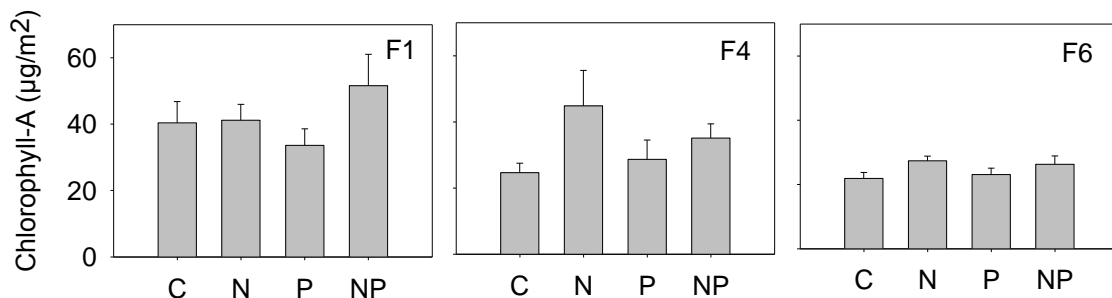

Figure 8. Mesocosm chlorophyll-A concentration relative to treatments at each site on Te Wairewa when assay dates are combined.
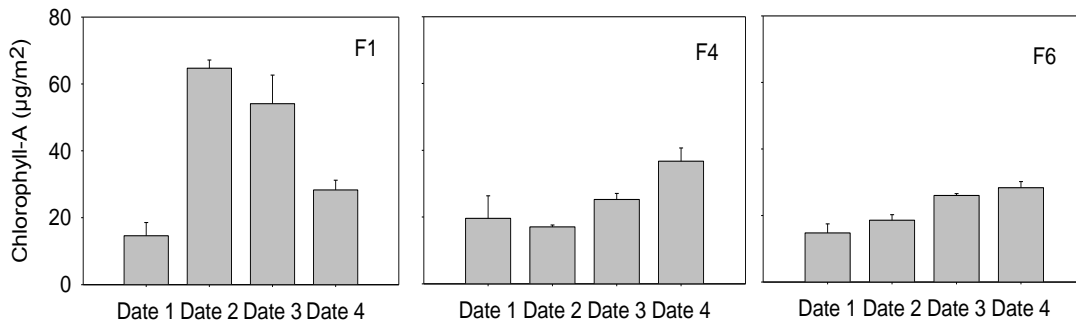
Figure 9. Mean chlorophyll-A concentration in control mesocosms at each site on each sampling date.

Examination of water samples from the mesocosms revealed differences in phytoplankton species assemblage at different sites and dates. During the first three assays between December 2010 and early February 2011, cubitainers from site F1 (the eastern, freshwater end of the lake) contained predominantly motile unicellular green algae, with fewer numbers of diatoms and 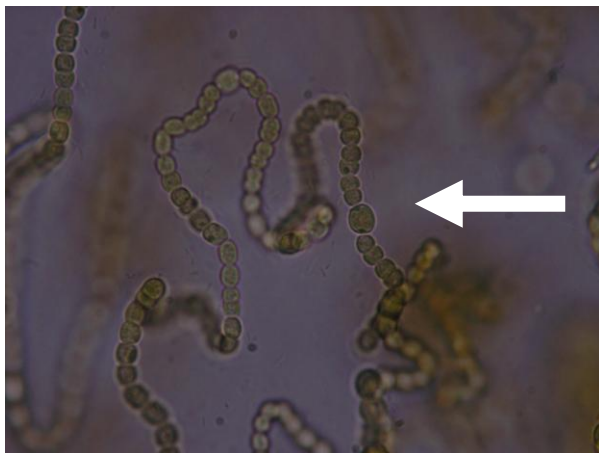picocyanobacteria. However, in the final assay (mid February 2011) cubitainers were dominated by heterocystous *Anabaena* instead of unicellular green algae (Figure 10). Cubitainers from F4 and F6 predominantly contained diatoms, picocyanobacteria and fungal strands and their composition did not change throughout the summer.

Figure 10. *Anabaena sp.* collected during a small bloom in Te Wairewa in late February, 2011. The arrow indicates a heterocyst; where nitrogen fixation takes place.

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DISCUSSION

Blooms in Te Wairewa were generally characterized by calm weather, shallow lake depths, relatively saline water, decreases in the nitrogen to phosphorus ratio and massive increases in nutrients. Blooms were preceded by changes in catchment stream chemistry. Because these factors characterizing bloom conditions occurred together, I could not absolutely determine which factor was more strongly associated with, or more likely to be causing lake blooms in this analysis. These factors, particularly those that are within the reach of lake management, such as lake depth, salinity, and nutrients, individually deserve further investigation. However, I did find that Te Wairewa was most consistently limited by nitrogen in nutrient addition assays, and also, that internal loading processes associated with calm weather conditions were likely to support phytoplankton blooms.

Nitrogen limitation in Te Wairewa: Nitrogen limiting conditions within the lake may give nitrogen fixing cyanobacterium a competitive advantage over other phytoplankton, if other factors do not limit their growth (Schindler 1977, but see Downing et al. 2001). Interestingly, both production and the effect of nitrogen and phosphorus addition were variable over sites on the lake, with the highest rates of production in the eastern, macrophyte-dominated, freshwater end of the lake coinciding with co-limitation between nitrogen and phosphorus, as opposed to the nitrogen-only limitation observed at the other two sites. There are several possible explanations for this. Macrophytes may drive this pattern by reducing sediment mobility and taking up nutrients, reducing concentrations of available nutrients in the water column. In addition,

the lower salinity at this end of the lake may reduce the bioavailability of phosphorus (Paludan et al. 1999).

While I found that nitrogen was primarily limiting production within the lake mesocosms, the range in lake N:P ratios indicated that both phosphorus and nitrogen limitation was likely within the lake over the 17 years of water quality sampling. High lake N:P ratios are considered to generally indicate phosphorus limitation, while low ratios indicate nitrogen limitation (Guildford et al. 2000, Perrone et al. 2008). Total N:P ratios are not a wholly reliable indicator of which nutrient is limiting, as they do not always strongly correlate with bioavailable N:P ratios (Beardall et al. 2001). However, given the large range of nitrogen and phosphorus concentrations in the lake over time, it is likely that nutrient supply and limitation within Te Wairewa is very dynamic. Several studies of nutrient limitation in lakes have found that nitrogen and phosphorus can both limit plankton biomass at different points in time within the same lake (Vrede et al. 1999, Ramírez-Olvera et al. 2009, Davies et al. 2010). Therefore, it is likely that phytoplankton growth in Te Wairewa is not always limited by nitrogen.

Nutrient supply mechanisms: Of the hypothesized nutrient supply mechanisms, internal loading processes associated with calm weather conditions were more likely to support phytoplankton blooms than external inputs of nutrients or loading processes associated with wind. My reasons for this conclusion are firstly, that nitrogen and phosphorus concentrations supplied from catchment streams are not sufficient to support large lake blooms, and secondly, blooms were associated with calm weather rather than windy weather. Below I evaluate the evidence for each of these mechanisms.

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Nitrogen and phosphorus concentrations in the Okuti and Okana Streams were not sufficient to support large lake blooms: Many eutrophic lakes have been remediated by reductions in external nutrient loading (Van der Molen et al. 1999, Istvánovics et al. 2001, Heisler et al. 2008). However, Te Wairewa is unlikely to respond quickly to reductions in external nutrient loading. A close examination of nitrogen and phosphorus supply to the lake from the Okuti and Okana Streams shows that although there are characteristic differences between bloom stream chemistry and non-bloom stream chemistry, these differences are more likely to represent parallel processes in the catchment and lake during bloom periods, rather than a causative link between catchment inputs and lake blooms. Stream nitrogen and phosphorus concentrations during blooms were higher than during non-bloom periods, and stream water also had a lower ratio of nitrogen to phosphorus. However, the size of the total nutrient input from both catchment streams is small relative to the amount rapidly appearing within the lake (a difference of a factor of ten) and of a magnitude that cannot be attributed to concentration associated with evaporation. For example, in a 15 day period between the 3rd and 18th January 2008, lake total nitrogen increased 8.8 mg/L (from 1.2 mg/L to 10 mg/L), and total phosphorus increased 2.16 mg/L (from 0.14 to 2.3 mg/L). This is an average increase of 0.59 mg/L per day of total nitrogen and 0.14 mg/L/day of total phosphorus. The Okuti and Okana Streams are reasonably sized third order streams, and during normal conditions, other overland flows are negligible. At the base flow rate I measured in the Okuti and Okana streams (Chapter 1) that are typical during bloom events ($\sim$0.2 m^3 s^{-1}) and an approximate lake volume of 6,270,000 m^3 (627 ha lake area and average depth of 1 m) the two streams combined

would take ~1 year to flush the lake. Extreme flood flows would contribute more nutrients to the lake, and have been found to influence phytoplankton assemblage and *Nodularia* blooms (Wilson 2008, Cook et al. 2010). However, I found no evidence that floods preceded blooms, as neither stream turbidity nor rainfall data were associated with blooms and lake nutrient concentrations were not unusually high before blooms. Additionally, flood conditions would have caused a decrease in salinity due to the influx of relatively fresh water, and instead I found an increase in salinity associated with blooms.

The differences in stream chemistry I found before and during blooms (higher phosphorus and lower nitrogen) are likely to be due to low base flow and increased primary productivity within catchment streams, which may be driven by the same factors which drive lake blooms, i.e., warm temperatures and calm conditions. During low base flow in a catchment rich in phosphorus, streams will have higher concentrations of phosphorus as they are not being diluted by overland flows. As there is more surface area of the stream bed available per unit water volume, uptake of nitrogen should be more efficient. In addition, macrophytes and algal growth should be higher in warm conditions, which would further improve uptake and reduce nitrogen concentrations in the water column.

Internal nutrient supply mechanisms associated with calm conditions are the most likely source of nutrients supporting large blooms in Lake Forsyth. As catchment stream inputs of nitrogen and phosphorus were not sufficient to explain the large and rapid increases in nitrogen and phosphorus concentrations, and my results indicate that wind associated re-suspension of sediments is not associated with blooms (longer distances of wind travel, and increases in lake turbidity relative to chlorophyll-A were not associated

with blooms), internal lake processes must therefore be providing phytoplankton with the nitrogen and phosphorus they require to reach bloom densities. Furthermore, the association between blooms, short wind runs and decreased catchment stream turbidity indicates that these internal processes occur predominantly during calm weather. While re-suspension of sediment and catchment floods do not explain the increases in lake nutrients associated with large blooms, they may be important for re-supplying nutrients on different time scales to those we sampled and analysed for. For example, lake turbulence due to wind may bring fresh sediment to the top, replacing sediment depleted in phosphorus, which can then later be more readily accessed by phytoplankton (Maceina et al. 1990, Qin et al. 2004).

Phosphorus bioavailability to phytoplankton depends on sediment composition and redox state; metal oxides, clay minerals and organic carbon complexes sorb phosphorus and decrease its bioavailability, while anoxic conditions increase its bioavailability via dissolution of iron oxides that predominantly bind the phosphorus (Paludan et al. 1999, Reynolds et al. 2001, Perrone et al. 2008). Anoxia, or at least very low oxygen concentrations are likely to occur at the lake bottom due to high respiration rates and a lack of mixing during blooms. The lake did not bloom strongly during the course of our nutrient addition experiments, but I observed extremely high rates of photosynthesis, shown by the extremely high range of dissolved oxygen concentrations and elevated pH. I also found a lack of lake mixing that would bring oxygen to the lake bed. Under these conditions, phosphorus would be more bio-available, possibly in quantities sufficient to supply the phytoplankton. Another factor that could enhance the bioavailability of phosphorus is lake salinity. Salinity generally decreases the strength of binding between

phosphorus and the metal oxides and organic carbon complexes within sediments (Paludan et al. 1999, Smolders et al. 2006). Therefore, during times of high salinity, such as during low lake levels or after opening the lake to the sea, phosphorus may be more bioavailabile. Further investigation of phosphorus binding processes relative to lake salinity and oxygen concentrations would be valuable in order to evaluate possible methods for lake remediation, such as manipulating lake openings to the sea, or adding a substrate to bind phosphorus in order to reduce its bioavailability (Reitzel et al. 2003, Mehner et al. 2008).

Compared to phosphorus, nitrogen is less likely to be sourced quickly, and in great quantities, from the lake bed because of its slower release during the processing and decay of organic matter by microbes (Saunders et al. 2001). Substantial nitrogen fixation must therefore be fulfilling cyanobacterial requirements. Both *Nodularia* and *Anabaena* have the ability to fix nitrogen from the air, and the presence of nitrogen-fixing heterocysts on samples of *Anabaena* taken from the lake in early February indicates they are actively fixing nitrogen, though it is not clear how significant this is relative to the lakes normal loading. Phosphorus supply from the lake bed and nitrogen from cyanobacterial fixation are the most likely mechanisms supplying blooms in Te Wairewa.

Cyanobacterial life history: Other aspects of cyanobacterial biology apart from nitrogen fixation may be important in determining bloom occurrence in Te Wairewa, such as the formation and germination of cyanobacterial resting phases (Akinetes). These resting phases form during unfavourable environmental conditions for cyanobacteria, and allow them to survive until conditions become favourable again to quickly develop into

blooms once conditions improve (Myers et al. 2010). Huber (1985) found that a combination of temperature, nutrients, light and salinity at the right levels allowed cultured *Nodularia spumigena* resting phases to germinate. In that investigation, germination occurred optimally at 22 $^{\circ}$C or higher, but rapidly above 16 $^{\circ}$C, required a small amount of phosphorus ($\geq$ 0.3 μM), an extended period of light (red light was most important) and salinities less than 20 ppt. Additionally, Huber found that blooms in the Peel-Harvey estuary (Western Australia) tended to occur 2 or 3 weeks after these conditions occur, generally after diatom blooms decompose after winter, releasing nutrients, the water clears, and temperature and salinity increase. Myers (2010) found similar factors were involved in the germination and growth of *Nodularia* in the Gippsland Lakes (Victoria, Australia), and that although resting stages only needed a small amount of phosphorous and nitrate to germinate, high concentrations of phosphorus and secondarily nitrate, improved their growth. Also, salinity was optimal between 5 and 25 ppt, though like Huber (1985) found, Nodularia also germinated and grew below these salinities (Myers et al. 2010).

These environmental conditions often occur within these limits at Lake Forsyth, making it an ideal environment for *Nodularia* colonization. Water temperature always reached 16 $^{\circ}$C or above in summer, and higher temperatures were associated with bloom periods. Salinity during blooms was within the optimal range for germination. We did not test directly whether light penetration was related to bloom occurrence, however, bloom periods were related to lower lake levels, which would increase light penetration to the lake bed. Phosphate and nitrate concentrations in the lake were rarely low. Our results show that large blooms are not as frequent in conditions outside these limits. This suggests

factors which contribute to *Nodularia* blooms in Australia are comparable to those in Te Wairewa, and highlights the importance of temperature, light penetration, salinity and nutrients in the initiation of *Nodularia* blooms.

It is important to note that while *Nodularia spumigena* has formed the most dramatic blooms in the lake over the time period of this study, because of the positive relationship between high nutrient concentrations and cyanobacterial or algal blooms (Downing et al. 2001), changes in environmental factors that reduce the suitability of the lake for *Nodularia* colonization (such as salinity or lake depth) will not necessarily result in a reduction in nuisance blooms of other phytoplankton species, with different optimal growth conditions, if nutrient concentrations remain high.

In summary, temperature, lake depth, calm conditions, moderately brackish salinity and high nutrient concentrations were important for the development of large cyanobacterial blooms in Te Wairewa. As the nutrients supporting blooms are being internally sourced, reductions in lake nutrients will be difficult to achieve, hampering remediation of the lake. However, while manipulations of temperature and calm conditions are outside the reach of management plans, lake depth, salinity and sediment binding processes could be targeted by lake management and deserve further investigation.

"Water is H_2O, hydrogen two parts, oxygen one,

but there is also a third thing, that makes water

and nobody knows what that is."

D.H. Lawrence

Chapter 3: Trophic state in Canterbury streams

ABSTRACT

The concept of stream eutrophication has only recently emerged, and because of this, the framework for monitoring stream eutrophication is still in development. Eutrophication refers to the development of highly a productive trophic state that threatens biodiversity. Variation in climate, geology, biology and land-use between regions may mean that the criterion for classifying stream trophic state also differs between regions.

To investigate the regional characteristics of stream trophic states relative to nationally and globally reported characteristics of stream trophic states, I measured community metabolism in 21 streams in the Canterbury region (South Island, New Zealand). The diel oxygen logging method, and both the propane injection and night-time regression methods to estimate re-aeration were used. Measured rates of metabolism, a good indicator of trophic state, were compared to national and international rates of metabolism from the literature. Canterbury streams were strongly heterotrophic, with rates of respiration ranging to the high end of those reported nationally and internationally (Canterbury respiration range: $1.42 - 33.33$ g O_2 m^{-2} day^{-1}; national: $0.34 - 55$ g O_2 m^{-2} day^{-1}; global: $0.1 - 84.8$ g O_2 m^{-2} day^{-1}). The autotrophic component of production in Canterbury was relatively low, varying between 0.04 and 2.78 g O_2 m^{-2} day^{-1}, compared to a national range of $0.1 - 29.2$ g O_2 m^{-2} day^{-1} and an international range of $0 - 58.9$ g O_2 m^{-2} day^{-1}. Production and respiration rates were highly correlated and scaled linearly from oligotrophic to eutrophic. My results support the use of stream metabolism as an indicator of stream eutrophication, and indicate that, if a framework for monitoring stream trophic

state is adopted, regionally specific health criterion would provide the most sensitive and accurate evaluation of stream health.

INTRODUCTION

Prolific weed growth, algal and cyanobacterial blooms, anoxia and loss of species are all symptoms of aquatic eutrophication, a process threatening ecosystems throughout the world (Vitousek et al. 1997, Smith 2003, Smith et al. 2009). Eutrophication is the process of increasing productivity within ecosystems, and this includes production by heterotrophic organisms, as well as by autotrophic organisms (Dodds 2006).

The concept of eutrophication emerged relatively early in the history of ecology. It probably originated as a product of increased pollution of water ways associated with population growth and rising consumption following the industrial revolution, coinciding with the expansion of scientific methodologies and awareness of sanitation. The first "eutrophication studies" were primarily concerned with heterotrophic eutrophication in lakes caused by sewage outfall, because of disease, odour and discoloration problems (Nixon 2009). Liebig's theory of nutrient limitation and Naumann's categorization of lakes by algal abundance in 1919 were key developments in linking autotrophic production with nutrients in aquatic ecosystems (Lewis et al. 2008). This was confirmed by several later studies, which identified phosphorus and nitrogen as the nutrients primarily limiting phytoplankton abundance in lakes (Lewis et al. 2008).

Further research has increased knowledge of production in lakes to the point that phytoplankton abundance can be now be reasonably predicted from nutrient concentrations (Dodds 2007), and lake trophic state can be monitored by a variety of tools,

including directly by chlorophyll-A concentration, nutrients and clarity or even indirectly by satellite imagery (Sheela et al. 2011).

Compared to lakes, the concept of eutrophication in streams is still developing. To illustrate this point, I performed a search in Google Scholar within the Biology, Life Sciences and Environmental Science area for articles with the terms "lake" and "eutrophication" or "stream" and "eutrophication" within the title (Search date: 7 September 2011). The search for "lake" and "eutrophication" returned 1050 hits in comparison to the search for "stream" and "eutrophication" which returned only 28 hits.

Two reasons probably explain this discrepancy. Firstly, eutrophication is not always obvious in streams, and does not always look like that in lakes (i.e., large blooms of algae and cyanobacteria and the associated hypoxic conditions). Flowing water makes surface algal blooms are much less common and produces more re-aeration than in lakes, so anoxia can be rare despite high nutrient concentrations. Secondly, although a method for measuring production in streams via changes in diel oxygen has been around for some time (Odum 1956), their application has been difficult until recently, involving either tedious diel Winkler titrations, closed system measurements which do not take into account stream heterogeneity, or else very expensive oxygen logging probes. Stream photosynthetic biomass does not correlate with production as closely as it does in the more autotrophic environment of lakes, so chlorophyll-A concentrations are a less reliable estimate of both autotrophic and heterotrophic production in streams (Dodds 2007, Baulch et al. 2009).

Recent improvements in the reliability and affordability of oxygen logging probes means that measuring production is now much less difficult, and has resulted in an

increased number of studies measuring stream productivity. Consequently, the analysis of stream trophic state is now approaching the reliability of lake methods. This has led to the development of predictive relationships between stream production and the factors that control it, and the beginnings of a meaningful framework for measuring and classifying trophic state in streams, so that it can be used as a response variable in stream management (Dodds 2007).

Using documented metabolic parameters, Young and colleagues (2008) used a percentile approach to classify trophic state, with the assumption that the low autotrophic and heterotrophic production associated with natural or very low intensity land use indicated good stream health. They defined production and respiration values representing "healthy" as being between the 25th and 75th percentiles of reference site distributions situated in relatively natural, unmodified catchments. Values of respiration between the 5th and 25th, and 75th and 95th percentiles were classified as "satisfactory" and values below the 5th and above the 95th percentile indicated "poor" stream health. Gross primary production (GPP) values were classified similarly, except that values below the 25th percentile were also included into the definition of "healthy" to recognize that low photosynthetic production does not necessarily mean poor health (Young et al. 2008).

As with lakes, classification into these categories is subjective, and at a regional scale, dependent on the range of stream trophic states available within that region. For example, an oligotrophic stream in Europe is likely to look different to an oligotrophic stream in a remote wilderness of Fiordland, New Zealand, or an oligotrophic stream in Honduras, because of the difference in geological, climatological, biological and human histories between regions. Because of this, regionally specific knowledge of trophic state

will be important to classify trophic state into meaningful categories relevant to management within that region.

The objective of this study was to determine the characteristics of stream trophic state within the region of Canterbury, New Zealand, and compare trophic state values within the region to national and international values. Many streams within the region are within agricultural land, with open canopies, high nutrients, and little riparian vegetation (M Greenwood, J Harding, D Niyogi, A McIntosh, in review), conditions which should favour in-stream photosynthesis rather than respiration of organic matter sourced from outside the stream (Hill et al. 1995, Young et al. 1999, Mosisch et al. 2001). Therefore, I predicted that Canterbury streams would be relatively autotrophic rather than heterotrophic (i.e., high photosynthetic production of carbon relative to in-stream respiration of carbon) in comparison to national and international studies.

METHODS

Study Area

Sampling sites were established in 21 streams throughout the Canterbury region of the South Island, New Zealand (Chapter 1, figure 1). This region area has a mild, temperate, maritime climate, with varying geology, topography, flora, fauna, and land use. To the east, the region contains a hilly inactive volcanic caldera that makes up the Banks Peninsula. The alluvial Canterbury Plains lie in the middle of the region and gradually slope up towards the foothills of the Southern Alps, which form the western boundary of the region. Streams range from low gradient, spring-fed agricultural streams, to high gradient streams in forested catchments with little human modification.

Canterbury has strong agricultural development, and extensive areas of land are used for grazing livestock at varying densities (Taylor et al. 1997, MacLeod et al. 2006). Dairy, beef and sheep farming are common, with smaller amounts of cropping, horticulture and exotic plantation forestry. Areas of relatively pristine and regenerating native forest are also present in reserves, but are almost absent from the Plains portion of the region.

I selected cobble bottomed stream reaches as sampling sites, across a gradient of riparian vegetation cover (from closed canopy streams to open canopy streams). Selected streams had a variety of nutrient concentrations, a mix of land-use intensities within the stream catchment, and were sampled in the late summer of 2010 between February and April. These were the streams studied in Chapter One.

Sampling methods:

I sampled stream metabolism using the open water diel oxygen logging method (Odum 1956), and estimated re-aeration by using propane injection as well as regressions of rates of night-time oxygen change against the oxygen saturation deficit. For a full description of the sampling methods and equipment used, see the methods section in Chapter One.

To obtain a representative set of stream metabolism measurements for comparison to my results, I conducted a literature review of 37 studies which reported metabolic parameters in a total of 280 streams throughout the United states of America (155), Australia (28), Europe (53), England (1), Puerto Rico (1), Venezuela (1) and New Zealand (44). Only studies which used the open water diel oxygen logging method of Odum (1956) and either one station or two station techniques to obtain metabolic rates, were selected. Studies were found by using search engines such as Google scholar and Scopus, and using the references of manuscripts to find other studies. I recorded production, respiration and production to respiration ratios (P:R) from each metabolism measurement in each study, when it was available, converting metabolic parameters into g O_2 m^{-2} day^{-1} for easy comparison with my own results where appropriate. Many authors reported their results in graphs rather than as raw data in tables; in these cases I estimated the value of the parameter from the scale. Several authors reported the range of metabolism they found in streams, but did not report each metabolism measurement. Because of this I was unable to include information about the distribution of their data beyond ranges into my results. These studies are marked with an asterisk in Table 1. Kruskal-Wallis tests were used to

compare stream metabolism in Canterbury to national and international values of stream metabolism.

RESULTS

Global stream metabolism: The maximum in-stream primary production recorded globally was 58.9 g O_2 m^{-2} day^{-1}, while the minimum was zero (first quartile: 0.33, median: 1.13, third quartile: 2.58 g O_2 m^{-2} day^{-1}). The maximum respiration was 84.8 g O_2 m^{-2} day^{-1}, while the minimum was 0.1 g O_2 m^{-2} day^{-1} (first quartile: 2.18, median: 4.10, third quartile: 7.00 g O_2 m^{-2} day^{-1}). Streams were generally heterotrophic, with P:R values ranging from 0 – 1.86 (first quartile: 0.10, median: 0.37, third quartile: 0.71, Figure 1 & 2, Table 1).

Figure 1. The distribution of GPP, respiration and P:R from measurements of metabolism in 21 streams within the Canterbury region of New Zealand (Canterbury) relative to other measurements made in New Zealand but outside the region (New Zealand), and to measurements of stream metabolism made globally but excluding New Zealand (World).

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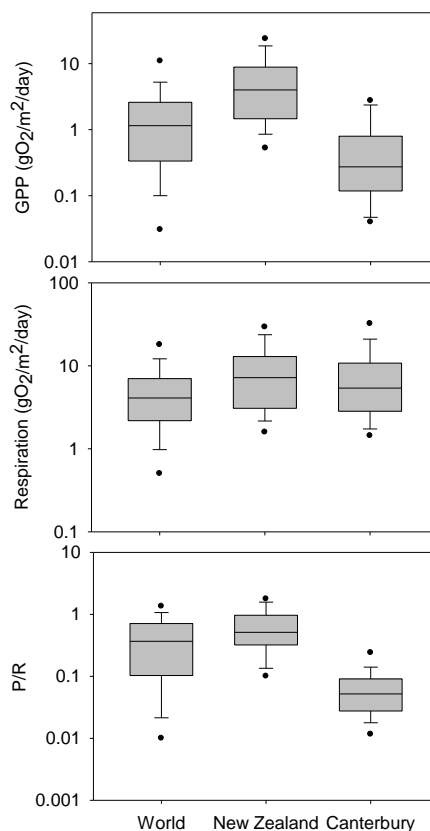
Metabolism in New Zealand streams: Values of gross primary productivity (GPP) from studies in New Zealand outside of the Canterbury region ranged from 0.1 to 29.2 g O_2 m^{-2} day^{-1} (first quartile: 1.47, median: 4, third quartile: 8.23 g O_2 m^{-2} day^{-1}), and the range was significantly different to global GPP (n 389, H 42.99, df 2, p <0.01). Respiration ranged from 0.34 to 55 g O_2 m^{-2} day^{-1} (first quartile: 3.38, median: 7.20, third quartile: 12.88 g O_2 m^{-2} day^{-1}) and was significantly different to the global distribution of respiration values (n 389, H 16.27, df 2, p <0.01) Streams were generally heterotrophic, and production to respiration ratios (P:R) ranged from 0 - 3.42 (first quartile: 0.32, median: 0.51, third quartile: 0.95 g O_2 m^{-2} day^{-1}, Figure 1 & 2, Table 1) and did not significantly differ from the global distribution of P:R (n 333, H 29.516, df 2, p <0.01).
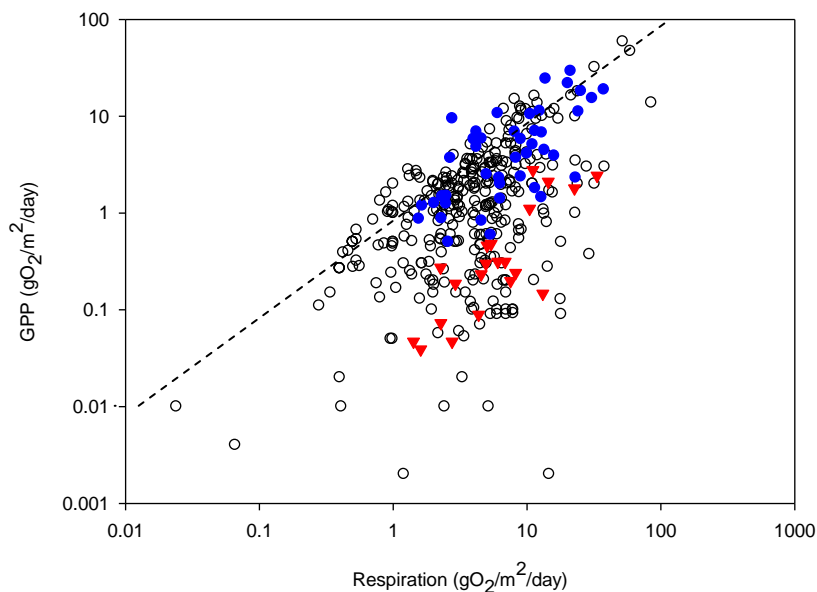

Figure 2. In-stream primary production (GPP) and respiration for 21 streams from the Canterbury region (New Zealand) relative to measurements from other New Zealand studies and international studies. Red triangles represent production and respiration at individual sites across Canterbury, blue dots represent primary production and respiration measurements in other New Zealand studies, and black circles represent measurements made internationally. The dashed line represents a production to respiration ratio of one.

Metabolism in Canterbury streams: Autotrophic production in Canterbury streams was generally lower than that found in other streams in New Zealand and globally (n 389, H 42.99, df 2, p <0.01 for both comparisons) while respiration was within the range of that found nationally or globally (n 389, H 16.27, df 2, p >0.05 for both comparisons). Gross primary production ranged between 0.04 and 2.78 g O_2 m^{-2} day^{-1} (first quartile: 0.15, median: 0.27, third quartile: 0.48 g O_2 m^{-2} day^{-1}), while respiration ranged between 1.42 and 33.33 g O_2 m^{-2} day^{-1} (first quartile: 2.91, median: 5.39, third quartile: 10.45 g O_2 m^{-2} day^{-1}; figure 1). Autotrophic production and heterotrophic respiration were strongly positively correlated (p <0.01 r^2=0.68, Chapter 1, Figure 4). All Canterbury streams were net heterotrophic (P:R < 1), and were more heterotrophic than other streams nationally and most streams globally (n 333, H 29.52, df 2, p <0.01 for both comparisons). The production to respiration ratio varied from 0.01 to 0.25 (first quartile: 0.03, median: 0.05, third quartile: 0.09; figure 1).

Table 1. Summary of documented rates of stream metabolism; gross primary production (GPP), respiration (R), and the production to respiration ratio (P:R), relative to their location. Studies which did not present raw metabolic measurements, only a range of values, are denoted with an asterisk.

Location	Land use	GPP (gO2/m2/day)	R (gO2/m2/day)	P:R	Reference
New Zealand					
5 streams in Taieri River catchment, SE New Zealand	Native and exotic forest, tussock and agriculture	0.6 – 3.7	2.0 – 5.4	0.1-1.5	(Young et al. 1999)
Taieri River, SE New Zealand	Native and exotic forest, tussock and agriculture	<0.3 – 9.6	0.7 – 9.8	Generally >1	(Young et al. 1996)*
23 lowland streams in the Waikato region, N New Zealand	Agriculture	0.5 – 29.2	1.6 – 37.5	0.07 – 1.87	(Wilcock et al. 1998)
15 sites in the Motueka river (upper South Island) & Mangaokewa (Central North Island) catchments, New Zealand	Native forest to pastoral farming.	0.1 - 7	0.34 – 16.5	0.1 – 1.5	(Young et al. 2009)
Australia					
Streams from Mary river in SE Queensland, Johnstone river in N Queensland and Northern Jarrah forest streams in SW Western Australia	Undisturbed, forested sites and disturbed open sites.	2.29 – 5.28	4.48 – 10.13	0.51-0.87	(Bunn et al. 1999)
5 sites on the La Trobe River Victoria, Australia	Forested to agricultural, urban and industrial	0.15 – 1.9	2.81 – 4.61	0.05 – 0.5	(Chaessman 1985)
Three sites on the lower Murray river, S Australia.	Forested, agricultural, urban	0.24 – 4.7	0.76 – 5.6	0.19 – 2.27	(Oliver et al. 2006)
4 sites on the Murrumbidgee river, S Australia	Agricultural, gum forest	0.14 – 2.67	0.1 – 3.14	0.2 – 1.2	(Vink et al. 2005)
Daly River, N Australia	Savannah vegetation	0.01 – 0.13	0.14 – 0.26	variable	(Webster et al. 2005)

Location	Land use	GPP (gO2/m2/day)	R (gO2/m2/day)	P:R	Reference
Spain					
13 streams in the La Tordera river catchment, NE Spain	Forested to urban and low to moderate intensity agriculture.	0.02 - 1.52	0.28 - 2.42	0.02 - 1.21	(Von Schiller et al. 2008)
19 Streams in Basque Country, N Spain	Generally intensive, including industrial, urban, rural tree plantations	2.7 - 11	6.3 – 42.6	Heterotrophic annually, but 3 autotrophic in summer	(Izagirre et al. 2009)*
Fuirosos stream, NE Spain	Forest	0.05 – 1.9	0.4 - 32	0.01-4.2 Average 0.16	(Acuña et al. 2004)
Italy					
Fosso Bagnatore stream, central Italy	Grassland, forest, urban, wastewater treatment plant	0.1 – 1.9	2.1 – 46.2	<0.002 – 0.33	(Ruggiero et al. 2006)
Switzerland					
River Spol & Val da la'Aqua, central Alps, Switzerland	Sub-alpine forest, below dam	0.7 – 7.1	0.9 – 5.2	0.2 – 2.4	(Uehlinger et al. 2003)
River Necker and River Thur, NE Switzerland	Forested, agriculture, urban in alpine catchment	<0.05 – 20.2	0.8 – 14.6	0.05 – 1.89	(Uehlinger 2000)
2 streams in the Macun catchment, E Switzerland	National park; alpine open-canopy streams	2.35 – 10.98	5 - 15	variable	(Logue et al. 2004)
Germany					
2 eutrophic streams: Deminitzer and Erpe Mill Brooks, near Berlin, Germany	Predominantly agricultural, urban	0.1 – 58.9	3.9 – 69.5	0.01 - 1.02	(Gücker et al. 2006)

Location	Land use	GPP (gO2/m2/day)	R (gO2/m2/day)	P:R	Reference
France					
Lezat and Montegue streams, Leze catchment, SW France	Predominantly agricultural, urban and forest also. Wastewater plant.	0 – 13.8	1.2 – 84.8	0 – 1.06	(Sánchez-Pérez et al. 2009)
England					
River Ivel, England	Agriculture, urban	0 – 1.2	3.28 – 19.85		(Edwards et al. 1962)
United States of America					
72 streams in nine regions in US and Puerto Rico	Agriculture, urban and reference	0.1 - 16.2	0.4 - 23.1	Predominantly heterotrophic	(Bernot et al. 2010)
8 streams across North American biomes	reference sites	<0.1 - 15	2.4 - 11	0.01 - 1.8	(Mulholland et al. 2001)
USA: South East					
6 tributaries of the Chattahoochee River, Atlanta, Georgia, USA	Urban and forest	0.43 – 2.38	1.31 – 8.72		(Meyer et al. 2005)
Ogeechee river, SE USA	Forested	0.49 – 13.99	3.7 – 11.5	0.09 – 1.3 Generally heterotrophic	(Edwards et al. 1987)
10 streams in Georgia, USA	Historical agriculture, now forested streams with localized soil and vegetation disturbance from military activities.	<0.01 - 1.75	0.3 - 16.3	Not stated	(Houser et al. 2005)
5 sites in the Ogeechee river basin, Georgia, USA	Forest, swamp	0.1 – 3.6	2.3 – 9.6	0.02 – 0.4	(Meyer 1990)

Location	Land use	GPP (gO2/m2/day)	R (gO2/m2/day)	P:R	Reference
4 streams; Rio Calaveras & Gallina ck (New Mexico),East Fork Walker Branch (Tennessee), Hugh White Creek (North Carolina), USA	Mountain meadows to forest	0.04 – 2.84	0.58 – 3.2	0.07 – 1.1	(Fellows et al. 2006)
18 Appalachian headwater streams in North Carolina and Virginia, USA	Gradient from forested to agriculture	0.1 – 0.23	4 – 7.5	0.01 – 0.18	(McTammany et al. 2007)
East and West Fork Walker Branch, Tennessee, USA	Deciduous forest	0.1 – 5.1	1.9 – 6	0.03 – 1.34	(Mulholland et al. 2006)
USA: North East					
10 Streams in the Hudson and Delaware catchments, near New York, USA	Mixed, including urban, agriculture and forest	0.4 - 4	1 - 8	<0.2 – 0.92	(Bott et al. 2006)
13 paired streams in 3 watersheds, Maryland, USA	Meadow or riparian forest	0.02 – 5.3	1.22 – 13.45	All heterotrophic	(Bott et al. 2006)
1 stream, SW Virginia, USA	Forested reference reach and semi open reach impacted by tailings from arsenic mine	0	1.3 – 5.6	0	(Lottig et al. 2007)
USA: North West					
11 streams from Grand Teton National Park, Wyoming, USA	Organic matter gradient, no canopy to forested	0.13 – 0.6	1.59 - 5.76	<1 All heterotrophic	(Hall et al. 2003)
3 streams in central Alaska, USA	Boreal forest streams, 1 burned, 2 unburned	0.9 – 3.5	0.2 – 8	heterotrophic	(Betts et al. 2009)
Portneuf River, SE Idaho, USA	Agriculture, forest, urban	0 – 0.2	1.5 – 2.2	0.1 – 0.5	(Marcarelli et al. 2010)

Location	Land use	GPP (gO2/m2/day)	R (gO2/m2/day)	P:R	Reference
USA: South West					
Gallina Creek and Rio Calaveras, central New Mexico, USA	Mountainous	0.2 – 1.7	2.3 – 14.7	0.03 – 0.25	(Fellows et al. 2001)
Puerto Rico					
Rio Mameyes, NE Puerto Rico	Forested	0.19 – 1.77	2.44 – 4.96	0.1 – 0.3	(Ortiz-Zayas et al. 2005)
Venezuela					
Rio Las Marias, Orinoco basin, Venezuela	Forested	0.4 – 0.9	0.6 – 1.7	0.26 – 0.64	(Taylor et al. 2006)*

DISCUSSION

Canterbury streams were strongly heterotrophic, with a close correlation between autotrophic and heterotrophic productivity. Relative to nationally and internationally reported rates of stream metabolism (Table 1), Canterbury streams ranged from having very low autotrophic and heterotrophic productivity to high autotrophic productivity and very high heterotrophic productivity, which reflects the variety of stream environments, and stream health, found within the region.

Canterbury streams and heterotrophy: Contrary to my prediction, autotrophy did not dominate in Canterbury streams. Although autotrophy increased with eutrophication, heterotrophy also increased, so that eutrophication in Canterbury streams was characterized by very high respiration as well as increased primary production. This was surprising, given that many streams sampled were intensely agricultural, with little or no riparian vegetation aside of grass to act as a substrate for respiration. Decreases in respiration due to a lack of riparian vegetation beside agricultural streams has been found elsewhere in New Zealand (Young et al. 1999). The source of the organic matter fueling high respiration rates in the region could be associated with soils, decaying autotrophic material, or effluent from agriculture (see Chapter 1, discussion). The prevalence of heterotrophy in the Canterbury region indicates that organic matter inputs have a particularly important role in the functioning of Canterbury streams compared to many streams throughout the rest of the world.

In addition to high respiration rates in Canterbury streams, low primary productivity also contributed to the dominance of stream heterotrophy. This might have been a seasonal effect due to sampling during mid-summer to early autumn. At this time of year there was a large biomass of photosynthetic material, but the shorter photoperiod at this time might have meant this was not actually a time of maximum photosynthesis. Alternatively, emergent plants on the stream margins, which respire underwater but release oxygen primarily into the air, might have caused us to underestimate production by our in-stream oxygen logging method. The influence of season and emergent plant oxygen dynamics do introduce some variation into estimates of stream productivity, which needs to be considered when developing an autotrophic health criterion.

The majority of national and international studies reviewed also reported heterotrophy of varying degrees, though not usually to the same degree as in Canterbury streams, and respiration and production scaled loosely together around the 1:1 ratio. There appeared to be an upper limit to primary production relative to respiration within streams, which is likely to reflect an upper physiological limit to the amount of oxygen produced by in-stream primary producers compared to the amount respired. In contrast, there was not a clear lower limit to primary production relative to respiration. Very few streams had no detectable photosynthetic production, and those that did were generally severely impacted by catchment activities, e.g. a waste water plant in an agricultural catchment (Sánchez-Pérez et al. 2009), or an arsenic mine (Lottig et al. 2007).

Stream productivity and health in Canterbury: Stream community productivity was a particularly good indicator of health in Canterbury for two reasons. Firstly, both autotrophic and heterotrophic production scaled as a power function, similarly to

Chlorophyll-A and nutrients in lakes (Downing et al. 2001, Dodds et al. 2007, Lewis et al. 2008). This dual response conveys fine scale information about changes in stream productivity, and the corresponding improvements or deteriorations in stream health over a very wide range of environmental conditions: from very oligo-trophic to eutrophic. Secondly, the relationship between production and respiration indicated the nature of stream eutrophication; i.e., as auto-eutrophic or hetero-eutrophic, as Dodds (2007) suggested. This distinction helped identify the stressors responsible for increasing eutrophication in Canterbury streams (organic matter, nutrients and removal of shading; Chapter 1).

Using Young and colleagues (2008) classification of stream trophic state, the range of primary production and P:R ratios I found in Canterbury streams all fell into the "healthy" category. However, according to respiration criteria, 29% of streams fell into the "poor" health category, 19% into the "satisfactory" category, and 52% fell into the "healthy" category. Considering the unwholesome appearance and severely impacted nature of several streams included in the study (M Greenwood, J Harding, D Niyogi, A McIntosh, in review), the respiration criteria of Young and colleagues (2008) far more accurately depicts stream health in the Canterbury region than the primary production or P:R ratio criteria, and highlights the importance of considering all aspects of metabolism to most accurately determine stream health.

A more sensitive autotrophic health criterion for Canterbury, given the characteristically low primary production in the region, could be based on the distribution of primary production in my results. Streams in this study represent a large gradient of health conditions, from healthy oligotrophic streams in relatively unmodified catchments,

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to strongly eutrophic streams within intensively farmed catchments, which make the distribution of my results a useful "yardstick" to compare health measurements in Canterbury with. Investigation of seasonal variation in productivity would further improve the accuracy of this criterion beyond mid-summer and autumn comparisons. The differences I found between regional metabolic rates and national or global metabolic rates indicates that regional calibration of stream metabolic health criteria would improve the detection and monitoring of changes in stream trophic state, and thereby improve detection and monitoring of land use effects on stream communities.

While measuring stream re-aeration is not yet completely straightforward, methods for estimating re-aeration reasonably accurately exist, such as night time regression of the saturation deficit and several empirical equations (Aristegi et al. 2009). This means that measuring stream metabolism can be as simple as putting a data-logging oxygen probe into a stream for 24 hours, then downloading it into a spreadsheet formatted to calculate metabolic parameters.

Given the feasibility of making such a measurement, sampling stream metabolism would provide valuable information for biological impact assessments.

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