Phytoplankton nutrient limitation in Lake Rotorua

ERI Report Number 157

Client report prepared for Bay of Plenty Regional Council
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2022

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Cite report as:

Tempero, G.W. 2022. Phytoplankton nutrient limitation in Lake Rotorua. ERI Report No. 157. Client report prepared for Bay of Plenty Regional Council. Environmental Research Institute, School of Science, University of Waikato, Hamilton, New Zealand. 38 pp.

Cover image: Satellite image of Lake Rotorua during *Dolichospermum circinalis* bloom, 21 October 2020.

Reviewed by: *Approved for release by:*

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Executive Summary

Lake Rotorua is one of 12 lakes jointly managed by the Rotorua Lakes Council, Te Arawa Lakes Trust and the Bay of Plenty Regional Council under the Rotorua Te Arawa Lakes Programme. The lake is currently classified as eutrophic and a Trophic Lake Index (TLI) value of 4.2 has been set as an integrated target for lake water quality. A number of catchment and lake management strategies have been implemented to achieve the targeted TLI including land use changes, wetland enhancement, lake weed harvesting, sediment detainment bunds, sewage reticulation and alum dosing. Alum (aluminium sulphate) is commonly applied to freshwater and wastewater systems to remove phosphorus, reducing its availability for phytoplankton growth. The initiation of alum dosing to the Utuhina Stream in 2006 and the Puarenga Stream in 2010 was associated with a significant decline in water column dissolved reactive phosphorus (DRP) and improvements in water quality of Lake Rotorua.

The use of alum to control external and internal phosphorus loading has been identified as key component in the restoration of Lake Rotorua and recently observed improvements in water quality suggest that the lake could be transitioning to a more phosphorus limited state. Determination of phytoplankton nutrient limitation in Lake Rotorua was identified as a priority through the 2017 Plan Change 10 Science Review. An initial seasonal nutrient limitation study was carried out in 2019 with nutrient limitation assays conducted at 3-monthly intervals over the course of the year. Nitrogen limitation was indicated for the March assay and nutrient co-limitation for the December period, but results for the winter and spring periods were inconclusive. There has also been increasing recognition that nutrient availability in limnetic systems may vary in response to seasonal changes in external and external loading and even to isolated storm events.

The University of Waikato was contracted to investigate potential changes in nutrient limitation within Lake Rotorua at sub-monthly time-scales, and to determine if alum dose rates could be optimised to take advantage of periods of phosphorus limitation. Phytoplankton nutrient limitation growth assays were conducted on a fortnightly basis from mid-October 2020 to May 2021. In addition to determination of lake surface nutrient and chlorophyll *a* concentrations, triplicate 1 L phytoplankton samples were spiked with either phosphorus (0.1 mg-P L^{-1}), nitrogen (1 mg-N L^{-1}) or phosphorus (0.1 mg-P L^{-1}) and nitrogen (1 mg-N L^{-1}) and incubated for 5-days under a single light intensity of 100 µmol $m^{-2}s^{-1}$ PAR at lake surface temperature and photoperiod. Phytoplankton growth responses were measured as comparative chlorophyll *a*, comparative biomass and net biomass growth. Summarised results from the 16 assays along with the predicted nutrient state from the stoichiometric mass ratio of TN:TP are presented in the table below.

Under the test conditions nitrogen limitation was indicated for most of the summer months (December–March) and nutrient co-limitation during the spring and late autumn. Only short

(~2 weeks) periods of P-limitation were observed, one of which was associated with an intensive storm event at the end of March. These seasonal fluctuations in nitrogen and phosphorus supply are similar to those observed in other temperate limnetic systems. In the spring, external nitrogen and phosphorus loading is high, then decline in the summer as rainfall and associated inflows wane. During the summer, internal loading becomes more important in polymictic lakes due to repeated internal nutrient cycling from stratification and mixing events. This results in phosphorus limitation in the spring, transitioning to nitrogen limitation or colimitation (primarily nitrogen) in the summer, and then returning to phosphorus/colimitation during the winter due to increased nitrogen-loading from the catchment from increased catchment discharge.

Due to the modest periods of phosphorus limitation indicated by the assays, there appears to be little potential for optimisation of alum dose rates in order capitalise on natural periods of phosphorus limitation. Further, changes in phytoplankton community composition and abundance appear to be more strongly driven by physical environmental factors such as temperature, light and wind speed, than nutrient availability. Although alum dosing is effective in removing DRP from the Utuhina and Puarenga inflows, its assumed effectiveness in reducing internal phosphorus loading in Lake Rotorua requires further evaluation.

Summarised results from 16 nutrient limitation assays conducted fortnightly from October 2020 to May 2021. Results include ratio of total nitrogen (TN) to total phosphorus (TP), chlorophyll *a*, phytoplankton biomass and net phytoplankton growth. *Indicates nutrient limitation was indicated not statistically significant.

Assay date	Surface mass TN:TP	Chlorophyll *a*	Phytoplankton biovolume	Net biomass growth
19 October 2020	Co-limitation	Co-limitation	P limitation	P limitation*
1 November 2020	Co-limitation	Co-limitation	Co-limitation*	Inconclusive
16 November 2020	P limitation	Co-limitation	Inconclusive	Inconclusive
29 November 2020	Co-limitation	N limitation	Co-limitation	No limitation
13 December 2020	P limitation	N limitation	N limitation*	No limitation
5 January 2021	Co-limitation	N limitation	N limitation	N limitation
18 January 2021	Co-limitation	N limitation	Co-limitation	N limitation
2 February 2021	Co-limitation	N limitation	N limitation	N limitation
14 February 2021	Co-limitation	N limitation	N limitation	N limitation
1 March 2021	N limitation	N limitation	N limitation	N limitation
14 March 2021	N limitation	N limitation	N limitation	Inconclusive
28 March 2021	Co-limitation	N limitation	N limitation	N limitation
9 April 2021	Co-limitation	P limitation	P limitation	P limitation*
26 April 2021	N limitation	N limitation	Co-limitation	Co-limitation*
9 May 2021	P limitation	Co-limitation*	Co-limitation	Co-limitation*
23 May 2021	N limitation	Inconclusive	Inconclusive	P limitation*

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Introduction

Phytoplankton nutrient limitation

For shallow polymictic lakes, such as Lake Rotorua, management of nitrogen (N) and phosphorus (P) availability is central to controlling eutrophication (Smith et al. 2006, Abell et al. 2020). This is achieved through mitigation measures that reduce internal and external nutrient loading to the lake (Abell et al. 2020, Paerl et al. 2020). The ratio of water column N to P should also be considered when developing nutrient management plans, as driving down N in relation to P concentrations (i.e., <15:1 N:P stoichiometric ratio) may result in the formation of N_2-fixing cyanobacterial blooms (Smith and Schindler 2009). There is also evidence that driving up the N:P ratio may result in the proliferation of non-N_2-fixing *Microcystis* blooms, as observed in Lakes Erie and Balaton which have undergone extensive management actions for P control (Paerl et al. 2014, Paerl et al. 2020). In addition, chlorophyte species often out-compete slower growing cyanobacterial species in systems with high N loading, leading to chlorophyte blooms which can detract from aesthetic and recreational values of the lake (Jensen et al. 1994). If a eutrophication management strategy is to be successful, understanding the limiting (or co-limiting) nutrient(s) is imperative for management strategies to be optimally effective in controlling cyanobacterial blooms.

There has been increasing recognition that the quantity and stoichiometric ratios of external and internal nutrient loading to aquatic ecosystems can vary seasonally, which can drive changes in nutrient limitation over time. For example, nutrient loading from inflows often reflects seasonal trends in precipitation and evapotranspiration by catchment vegetation (Mulholland and Hill 1997, Frost et al. 2009). Changes between high winter/spring and low summer discharges can alter the extent to which algae in downstream aquatic ecosystems are limited by N or P (Bukaveckas and Crain 2002, Royer et al. 2006, Vanni et al. 2006). In agricultural catchments, high winter/spring stream discharges often result in high N loading to downstream systems, which can promote P limitation (Mulholland and Hill 1997, Williamson et al. 2018). In contrast, lower stream discharge during the summer often reduces nutrient loading and N:P ratios, thereby promoting N limitation (Williamson et al. 2018). However, storm driven high discharge events may reduce N:P for short periods of time as stream P often increases disproportionately compared to N during storm events (Williamson et al. 2018, Kelly et al. 2019). Internal nutrient loading of lakes is also seasonally influenced, as increased surface temperatures during the summer often results in thermal stratification and the formation of anoxic conditions in the hypolimnion, resulting in release of N and P from bottom sediments. In shallow, polymictic lakes, wind driven mixing results in periodic release of nutrients over the summer-autumn, often sustaining phytoplankton growth. In comparison, deeper, monomictic lakes remain stratified for most of the year, only mixing

during the winter and releasing a single nutrient pulse that promotes spring phytoplankton blooms (Wilhelm and Adrian 2008, Von Westernhagen et al. 2010).

It has been proposed that recent improvements in Lake Rotorua water quality are a result of the alum dosing to the Utuhina and Puarenga inflows and a shift towards more frequent P limitation (Figure 1). However, the intensity and sustainability of alum dosing should be carefully weighed against the management of present and future nutrient loads from mitigating changes in catchment land use (Hamilton et al. 2015). Determination of phytoplankton nutrient limitation in Lake Rotorua was identified as a priority through the 2017 Plan Change 10 Science Review (Donald et al. 2019). The objective was to determine the role of the on-going alum dosing programme in achieving the long-term TLI target for Lake Rotorua, as well as providing improved understanding of the nutrient limitation status of the lake. The question of nutrient limitation was also raised through the Plan Change 10 hearing process, with particular emphasis on identifying if the lake was P limited, N limited or N and P co-limited. It is also possible that the lake's nutrient limitation status is actually variable due to seasonal changes in external and internal loading. An initial seasonal nutrient limitation study was carried out in 2019, with assays conducted four times over the course of the year at 3-monthly intervals. Nitrogen limitation was indicated for the March assay and nutrient co-limitation for the December period. The March N limitation was likely due to epilimnetic nutrient depletion during periods of summer stratification followed by release of hypolimnetic P during breakdown of stratification in the autumn. Similarly, co-limitation in December was likely due to epilimnetic nutrient depletion associated with stratification. Assays conducted in winter (June) and spring (September) were inconclusive due to light limitation and high variability in the assay data (Tempero 2020). Therefore, it was concluded that the nutrient status of Lake Rotorua likely varied, at least on a seasonal scale, but there was insufficient resolution to determine the temporal scale of these changes or specific environmental drivers.
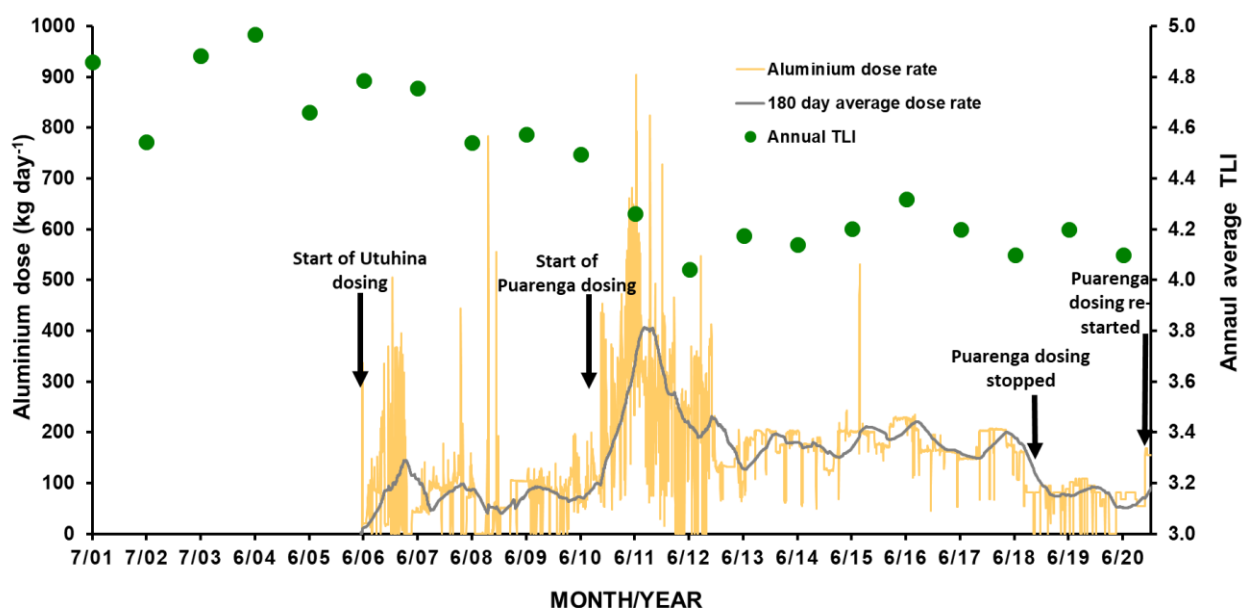
Figure 1. Daily aluminium dose rates to Lake Rotorua with mean annual trophic lake index (TLI) from 2001 to 2020. Blue dashed line indicates the TLI restoration target of 4.2 for Lake Rotorua.

Further investigation of nutrient limitation at sub-monthly scales over the spring-summer-autumn period could provide improved resolution of nutrient availability in relation to environmental perturbance and allow for assessment of more responsive nutrient limitation indicators such as DIN:TP. Increasing the number of nutrient limitation assays during this period could also provide improved understanding into cyanobacterial growth responses to nutrient addition and the dynamics between phytoplankton taxonomic groups.

The University of Waikato was contracted to undertake, phytoplankton nutrient limitation assays to meet the following objectives:

1. Determine the likely limiting macronutrient (N or P) or macronutrients (N and P) of the phytoplankton community assemblage in Lake Rotorua on a fortnightly basis over the spring-summer-autumn period.
2. Determine the concentrations of inorganic and total nutrients in relation to phytoplankton community composition at the same temporal scale.
3. Based on the findings of objectives 1 and 2 make recommendations as to the potential for adaptive alum dosing of inflows to Lake Rotorua in response to P limitation status.

Methods

Study site

Lake Rotorua (Figure 2) is the largest of 12 lakes jointly managed under the Rotorua Te Arawa Lakes Programme. It has a surface area of 80.6 km^2, a mean depth of 10.8 m (maximum depth 45 m), a total water volume of 0.85 km^3 with polymictic stratification patterns (Burger et al. 2007). A TLI target of 4.2 has been set for Lake Rotorua, which is considered representative of the lake's tropic state in the early 1960s, and considerably lower than that of the early 2000s (McBride et al. 2018a).
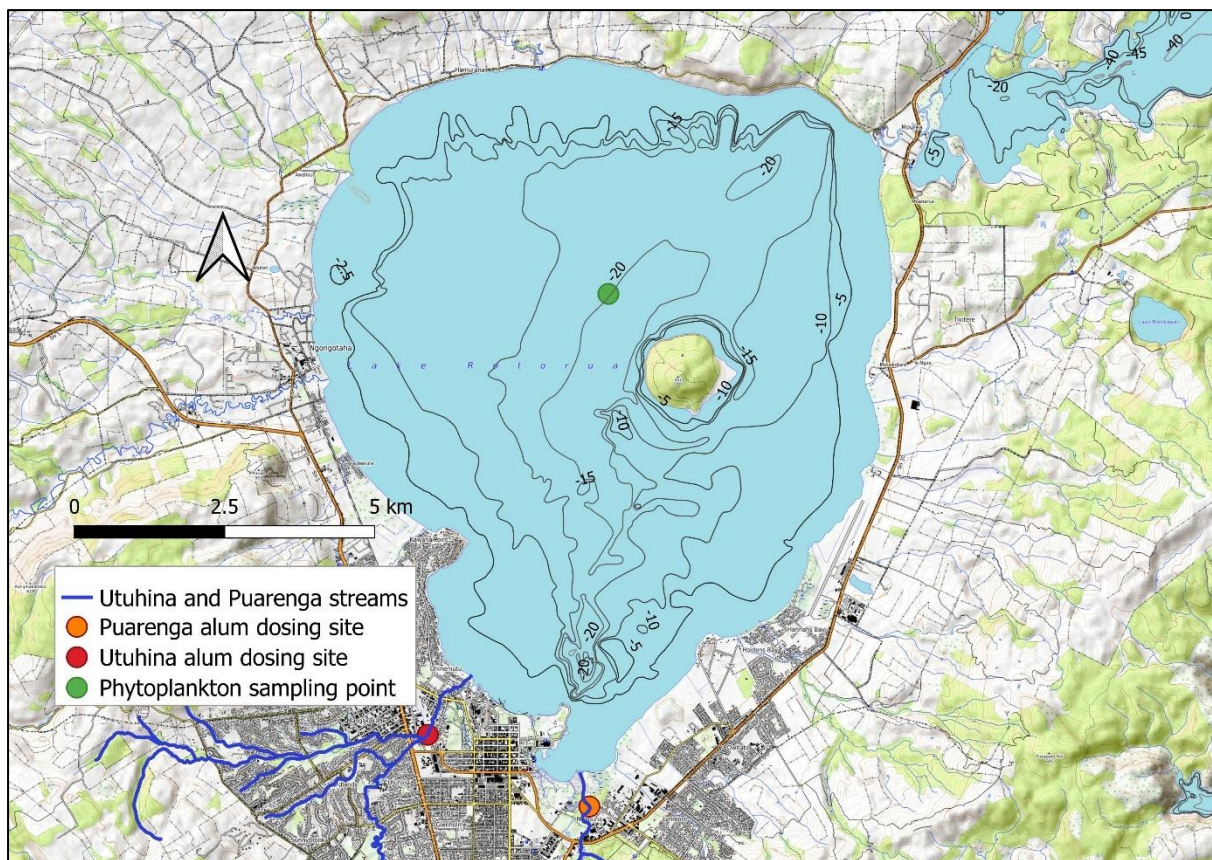
Figure 2. Lake Rotorua with locations of alum dosing stations on the Utuhina and Puarenga Streams. Samples for nutrient limitation assays were taken approximately 25 m from the Lake Rotorua monitoring buoy.

Environmental data

Water temperature and dissolved oxygen data from the Lake Rotorua monitoring buoy were provided by Limnotrack. Daily rainfall records for the Rotorua catchment were obtained from the NIWA Cliflo database (Station# 1770).

In addition to lake nutrient and chlorophyll *a* concentrations, phytoplankton nutrient limitation was assessed by determination of phytoplankton growth from changes in chlorophyll *a* and total algal biovolume following nutrient addition. Assays included the addition of both N and P to determine nutrient co-limitation. Lake sampling and growth assays were conducted a total of 16 times from October 2020 to May 2021 (Table 1).

Table 1. Sampling date and conditions of phytoplankton growth assays to determine nutrient limitation in Lake Rotorua. Water temperature (2 m depth) and photoperiod were set to match prevailing seasonal attributes.

Date	Temperature (°C)	Photoperiod (hh:mm)
19 October 2020	15.0	13:30
31 October 2020	17.0	13:40
16 November 2020	17.5	14:20
29 November 2020	18.0	14:35
13 December 2020	19.0	14:45
05 January 2021	20.5	14:45
18 January 2021	21.0	14:25
02 February 2021	21.0	14:00
14 February 2021	21.0	13:35
01 March 2021	21.0	13:00
14 March 2021	20.0	12:20
28 March 2021	19.0	11:50
09 April 2021	18.0	11:20
26 April 2021	17.0	10:40
09 May 2021	15.0	10:15
23 May 2021	14.0	9:50

Lake sampling

Lake water sampling was conducted approximately 25 m from the Lake Rotorua automated monitoring buoy (WGS84, Lat. -38.071479, Long. 176.270123). Water samples from the near-surface (2 m depth) and hypolimnion (15 m depth) were analysed for total nitrogen (TN), total phosphorus (TP), dissolved reactive phosphate (DRP), nitrate, nitrite and chlorophyll *a* concentrations. Approximately 20 L of water was retrieved from the near-surface (2 m depth) and immediately filtered using a 100 µm net to remove large zooplankton capable of reducing phytoplankton biomass due to grazing. Nutrient samples and the filtered water were then placed in a dark chilled container and transported back to the laboratory for analysis.

Phytoplankton growth assays

Triplicate 1 L phytoplankton growth assays were incubated for 5-days under a single photosynthetically active photon flux of 100 µmol $m^{-2} s^{-1}$ PAR (Solar system 550, California Lightworks) with photoperiod adjusted to match seasonal conditions along with equivalent in-lake temperatures (2 m depth). Phosphorus as K_2HPO_4 was added to a final concentration of 0.1 mg-P L^{-1} to the +P treatment and N as $NaNO_3$ to a final concentration of 1 mg-N L^{-1} to the +N treatment. An additional combined +N and +P treatment group was conducted for assessment of co-limitation. Samples were kept in suspension using an orbital shaker and daily gentle hand mixing.

Lake nutrient concentrations were analysed by Hill Laboratories using a Flow Injection Analyser 8500 Series II (FIA+ 8000 Series, Zellweger Analytics, Inc. Hach). Phosphate was analysed using LACHAT QuickChem method 31-115-01-1-H; ammonium was analysed using LACHAT QuickChem method 31-107-06-1-B and LACHAT QuickChem Method 31-107-04-1-A was used to analyse nitrate/nitrite. Limits of detection were 0.004 mg N L^{-1} for NO_2, NO_3, 0.01 mg N L^{-1} for NH_4 and 0.004 mg P L^{-1} for DRP.

For chlorophyll *a* analysis, 50 mL was filtered onto a glass fibre filter (GF/C: nominal pore size 0.45 µm, 25 mm) and then stored frozen (-20°C) in the dark before extraction with 90% buffered acetone. The samples were steeped for 24 h at 4°C before centrifuging at 3300 rpm for 10 minutes. Five ml of supernatant was then fluorometrically analysed using a Turner Designs 10-AU-005-CE fluorometer (Sunnyvale, CA, USA) calibrated against pure chlorophyll *a*. Differences between chlorophyll *a* concentrations were determined using two-way ANOVA (factors were time and nutrient treatment), followed by Tukey's post-hoc tests

Phytoplankton samples (50 mL) were taken at the beginning (day 0) and end (day 5) of the growth assay, and preserved with Lugol's iodine. Phytoplankton species abundance was determined from 10 mL aliquots allowed to settle in a tubular plankton chamber (Hydro-bios, Denmark) for 24 hours prior to counting. Species were identified to the lowest possible taxonomic level using an inverted microscope (Olympus, Ix71, Japan) at either 400X or 200X magnification in a single transect. The 8-10 most numerically dominant species for each replicate were identified and enumerated. Where filamentous and colonial species were highly abundant cell counts from were derived from the average number of cells in a subsample of 30 plankton units. Species densities were converted to algal biovolume ($µm^3$ mL^{-1}) using standard values from published literature (Dryden and Vincent 1986, Olenina et al. 2006, Rimet and Druart 2018). Differences in biovolume were determined using two-way ANOVA followed by Tukey's post-hoc tests. Net rates of phytoplankton growth over the incubation period, based on species biovolume, were calculated using the equation:

$$r_n = \frac{\ln(N_t/N_0)}{t} \text{(Reynolds 1997)}$$

where r_n is the growth rate (day^{-1}) and N_t and N_0 are cell densities at times t and 0, respectively. Differences in biovolume and phytoplankton biovolume linear growth rate were determined using one-way ANOVA followed by Tukey's post-hoc tests.

Phytoplankton bioassay outcomes were classified according to the nutrient limitation categories defined by Harpole et al. (2011), and illustrated in Figure 3. The responses include:

- *Single nutrient (N or P) limitation*; a response to only one of the nutrient treatments (+N or +P) and the response to the combined treatment (+N+P) is no different (Figure 3A).
- *Serial limitation (N or P)*; the response is to only one of the single nutrient treatments (+N or +P) but a larger response to the +N+P treatment (Figure 3B).
- *Independent co-limitation (primary N or P)*; a response to both single nutrient treatments and a larger response to the +N+P treatment; the single treatment with the larger response indicates the primary limiting nutrient (Figure 3C).
- *Simultaneous co-limitation;* response only to the +N+P treatment (Figure 3D).
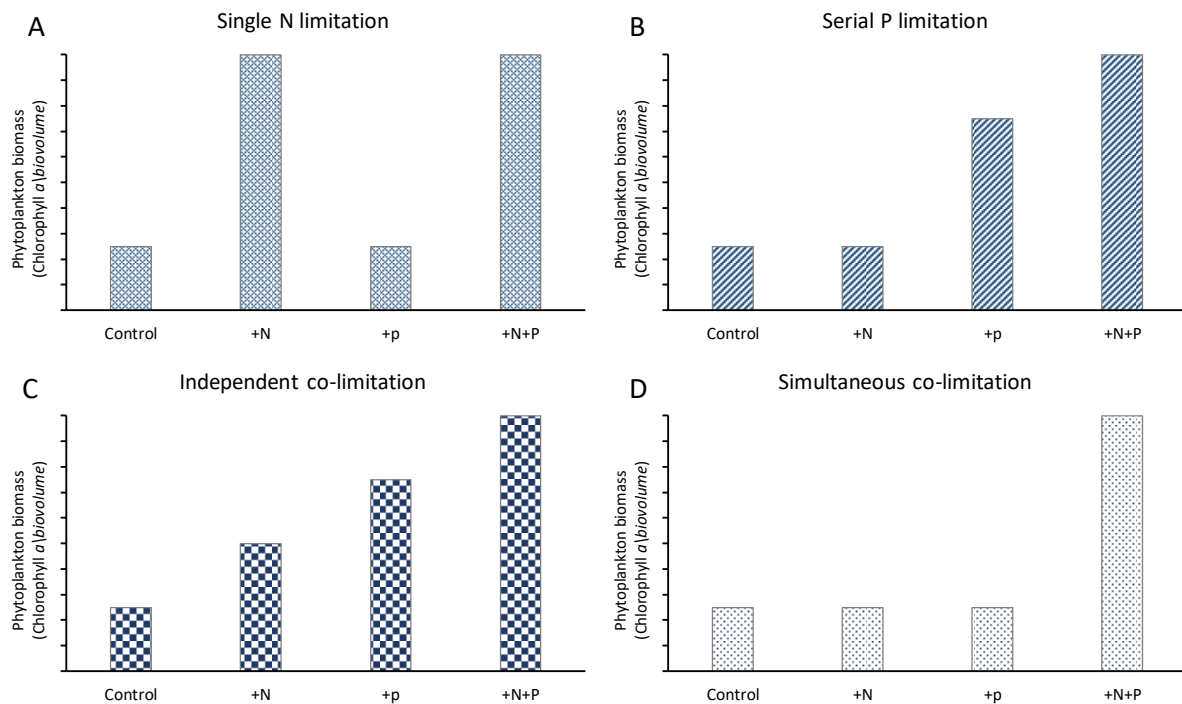
Figure 3. Example biomass growth response patterns. These patterns correspond to a subset of the nutrient limitation categories defined by Harpole et al. (2011). A) Single N limitation: a response to only one of the single treatments, in this example +N and the response to the +NP treatment is no different. B) Serial P limitation: a response to only one of the single nutrient treatments, in this example +P and a larger response to the +NP treatment. C) Independent co-limitation (primary P): a response to both single nutrient treatments with a larger response to +P and an even larger response to the +NP treatment; D) Simultaneous co-limitation: a response only to the +NP treatment. No nutrient limitation: no response to any nutrient treatment (not shown).

Results

Lake stratification and rainfall

Water temperature and dissolved oxygen concentration data were measured at 15-minute intervals by the Lake Rotorua monitoring buoy. The data were graphed to determine periods of stratification between 1 October 2020 and 31 May 2021 (Figure 4). Repeated periods of stratification and mixing were evident from October 2020 to early March 2021 followed by holomixis through to the end of the sampling period in May 2021.
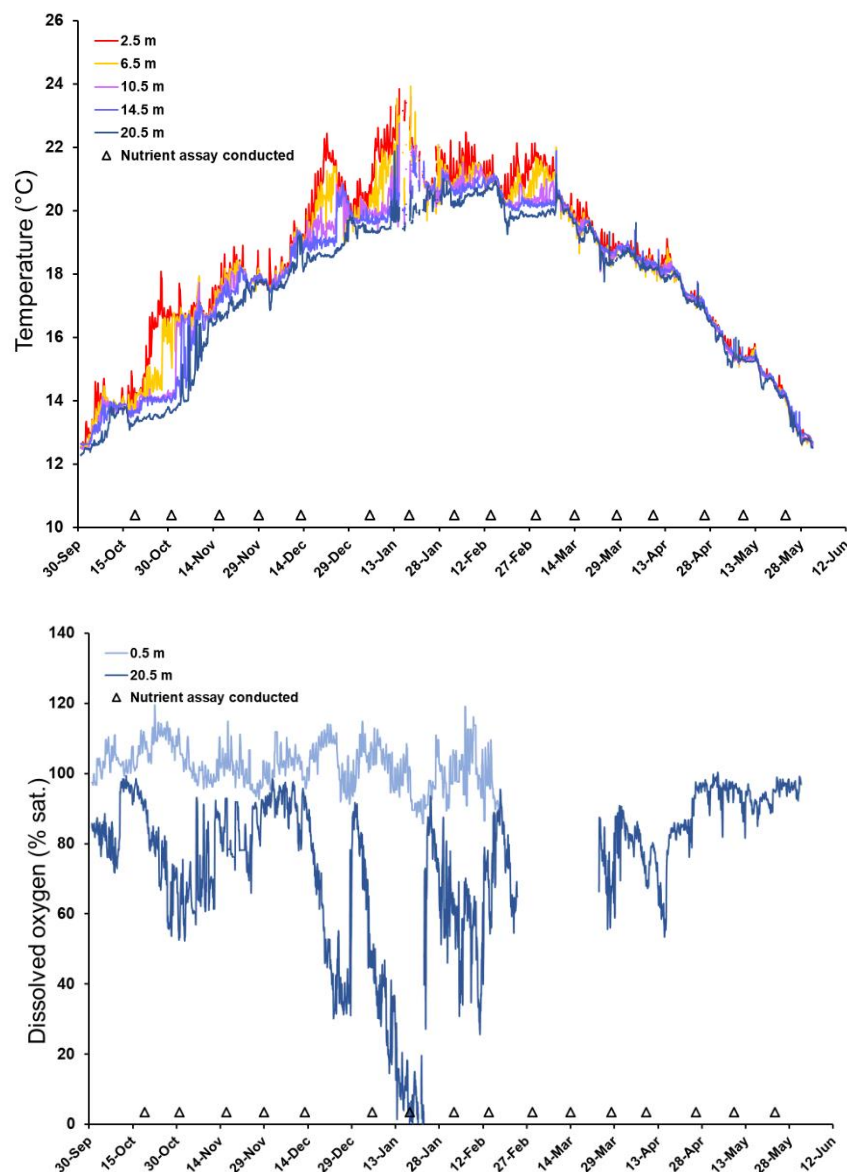
Figure 4. Lake Rotorua water temperature (top) and dissolved oxygen concentrations (bottom) from 1 October 2020 to 31 may 2021. Sampling dates for nutrient limitation assays are indicated by open triangles. Data provided by Limnotrack.

The hypolimnion was transiently hypoxic from December 2020 to February 2021 with a small period of anoxia occurring from mid to late January during the period of strongest stratification (Figure 4). Further analysis was limited due to the surface (0.5 m) dissolved oxygen sensor malfunctioning on 17 February 2021 and the bottom (20.5 m) sensor was not operational between 23 February to 23 March 2021.

Rotorua catchment daily rainfall from 1 October 2020 to 31 May 2021 is presented in Figure 5. Of note was an unusually intensive rainfall event which occurred on 31 March 2021, while the magnitude of this event was similar to other rainfall events during the study period, >30 mm of the total occurred in a 1–2-hour period resulting in large scale surface runoff.
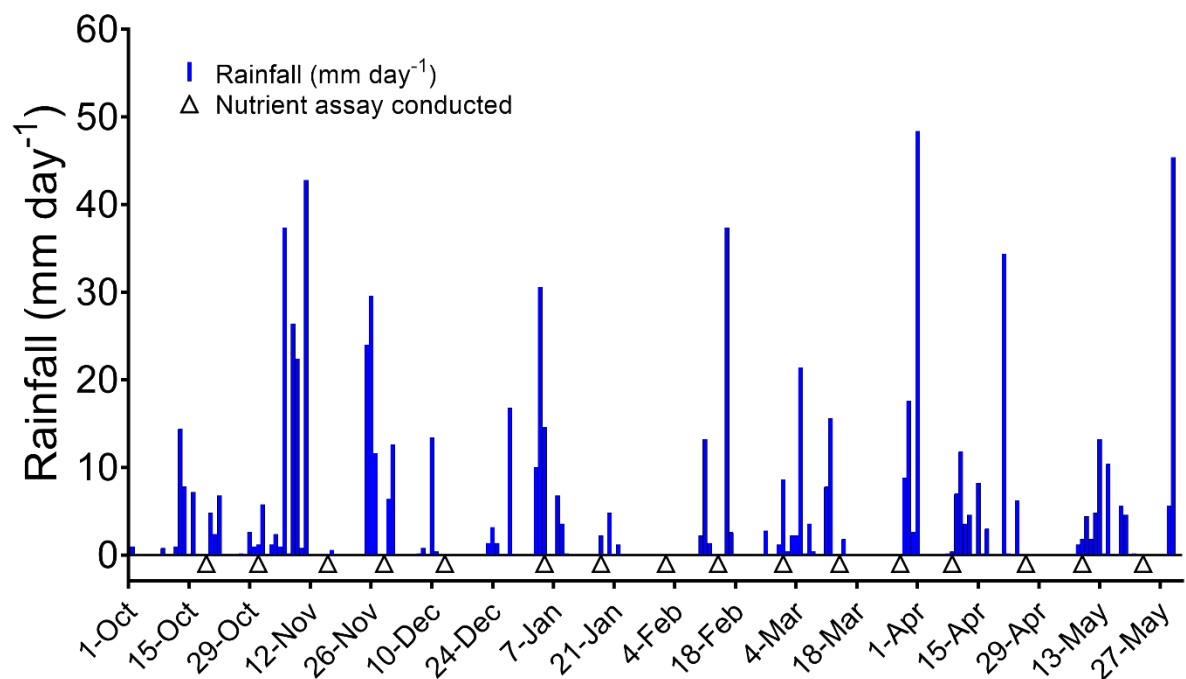
Figure 5. Rotorua daily rainfall (mm day^{-1}) from 1 October 2020 to 31 May 2021. Sampling dates for nutrient limitation assays are indicated by open triangles. Data retrieved from NIWA Cliflo database 2021, Rotorua Airport Station #1770.

Lake nutrient concentrations

Transient increases in hypolimnetic dissolved inorganic nitrogen (DIN) concentrations and DRP were observed in mid-to-late February and early April 2021. The February increase in hypolimnetic dissolved nutrients was likely related to the extended period of hypoxia in January, although this release did not appear to notably influence epilimnetic nutrient availability. The April peak followed the intensive rainfall event on 31 March 2021 (Figure 6). Epilimnetic concentrations of DIN and DRP were generally near or below analytical detection levels until early April. Total nitrogen and total phosphorus concentrations were similar between epilimnetic and hypolimnetic waters, apart from peaks in TN during mid-November and early May. Also of note, was a four-fold increase in lake TP from January to the end of March, although there was little change in TN (Figure 6).

Changes in the stoichiometric ratio of TN to TP in the epilimnion and hypolimnion are presented in (Figure 7). Based on the TN:TP, rapid switching between phosphorus limitation and nitrogen limitation is indicated from October to December 2020, followed by an extended period of nitrogen limitation from January to the end of March 2021 and associated with increasing epilimnetic TP. Nutrient ratios become unstable again at the end of March until the end of the study in May. Examination of alternate indicators, utilising dissolved nutrient ratios such as DIN:DRP was not viable as the majority of values were below the analytical detection limits and did not provide the required resolution.
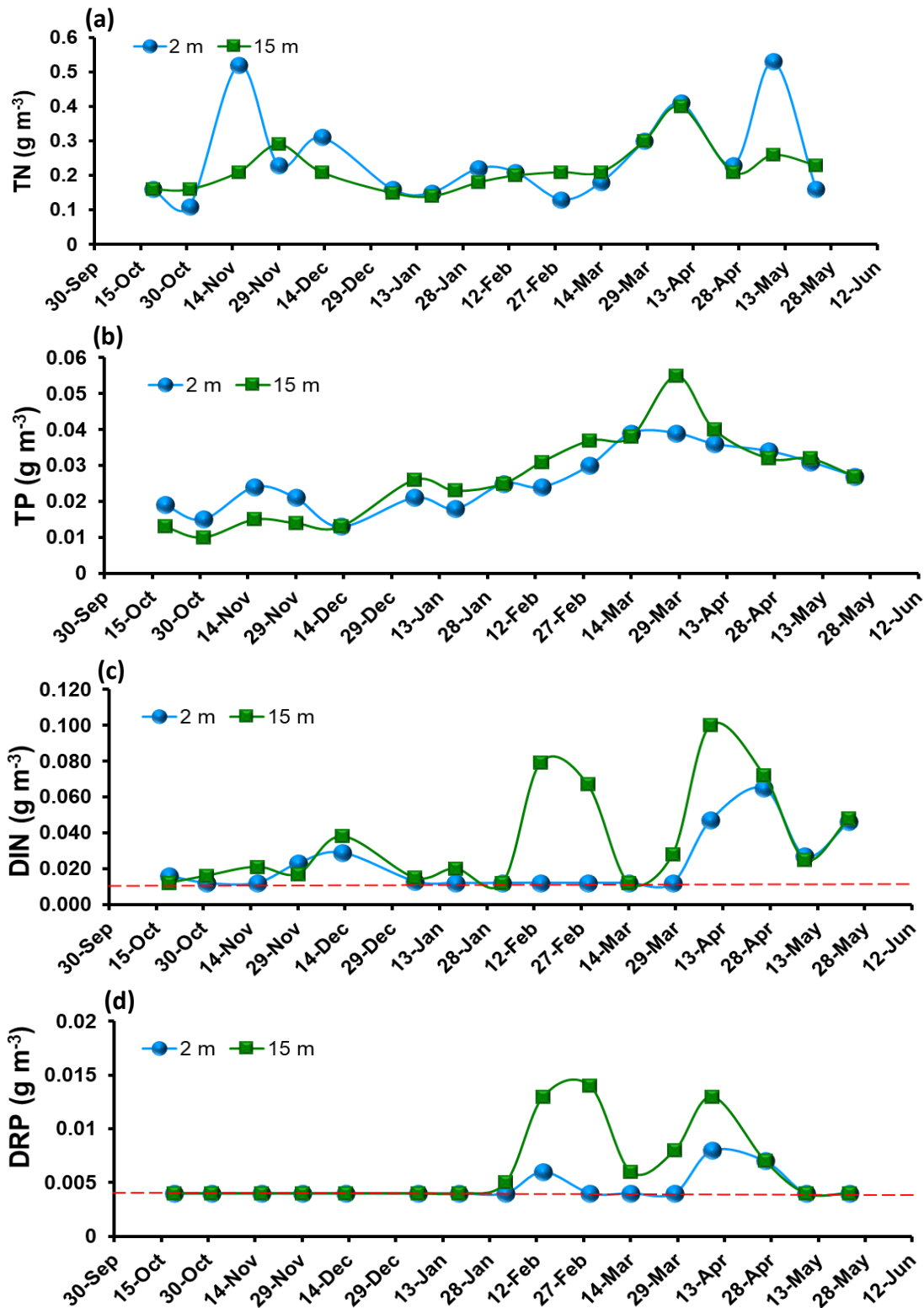
Figure 6. Lake Rotorua nutrient concentrations, (a) total nitrogen (TN), (b) total phosphorus (TP), (c) dissolved inorganic nitrogen (DIN) and (d) dissolved reactive phosphorus (DRP) sampled from the epilimnion (2 m) and hypolimnion (15 m) from 19 October 2020 to 23 May 2021. Red dashed line indicates analytical detection limit.
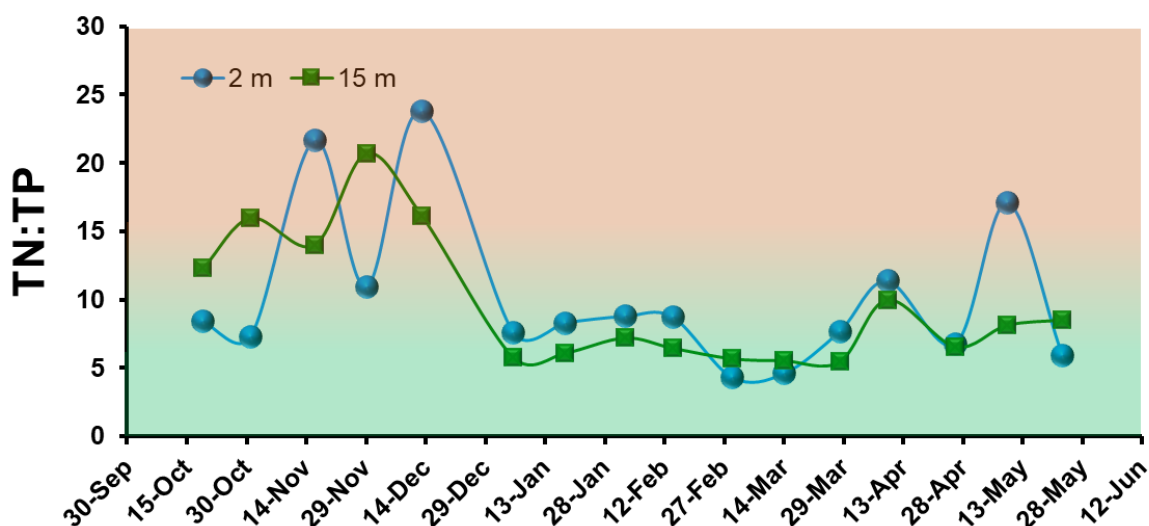
Figure 7. Mass ratio of total nitrogen (TN) to total phosphorus (TP) at 2 m and 15 m depth from 19 October 2020 to 23 May 021. At <7 (green) nitrogen limitation is indicated and >15 (orange) phosphorus limitation (Abell et al. 2010).

Lake chlorophyll *a*

Lake Rotorua mean chlorophyll *a* concentrations at 2 m and 15 m depth were 16.4 (±1.6 SEM) mg m^{-3} and 13.8 (±2.0 SEM) mg m^{-3}, respectively. A cyclic pattern in chlorophyll *a*, particularly in the hypolimnion (Figure 8), was observed over the course of the study, with fluctuations increasing over time.
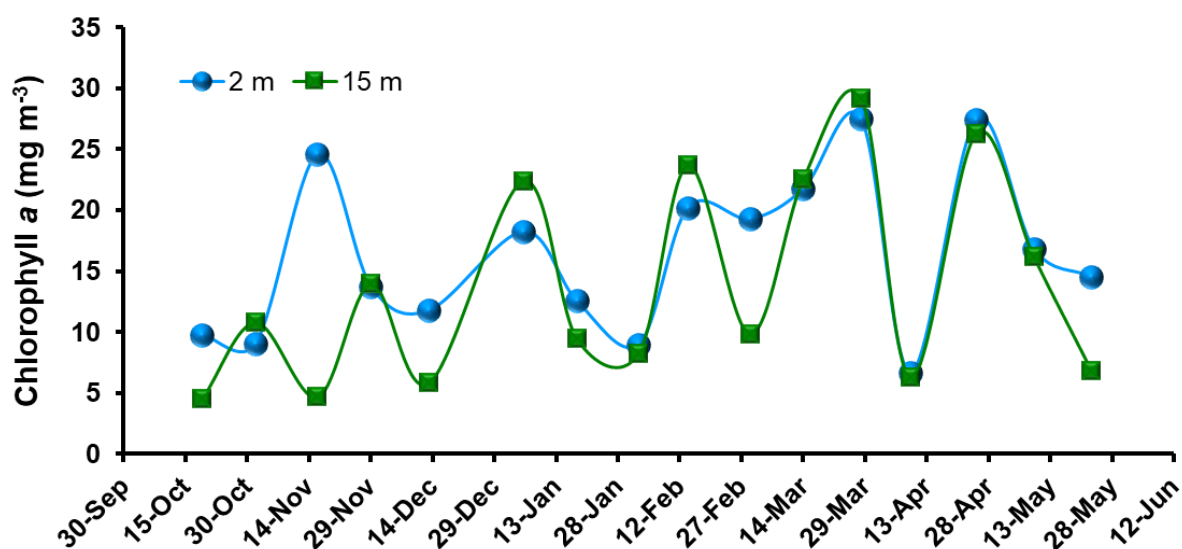
Figure 8. Lake Rotorua chlorophyll *a* concentrations sampled from 2 m and 15 m depth at approximately 2-weekly intervals 19 October 2020 to 23 May 2021.

Phytoplankton nutrient limitation assays were conducted at approximately fortnightly intervals from 19 October 2020 to 23 May 2021. Growth responses to nutrient addition including chlorophyll *a*, phytoplankton biomass and net phytoplankton growth rates are summarised in Table 2 and graphed individual assay responses are presented in Appendix 1. Changes in the limiting nutrient(s) were observed throughout the monitoring period with phosphorus limitation, nitrogen limitation and co-limitation present at various times. The nutrient mass TN:TP often had poor agreement with the nutrient addition assays, possibly due to a high proportion of refractory N and P in the lake. A *Dolichospermum circinale* (Cyanophyta) bloom had established more than a month before the start of the study and persisted through until mid-November. Net biomass growth results were often inconclusive during this period, as cyanophyte growth responses were limited under laboratory conditions, but constituted the majority of the lake's phytoplankton biomass (Figure 9) Phosphorus limitation was briefly indicated in mid-October, but was followed by a trend to towards N limitation as the lake became first co-limited, then N limited by mid-December. The dominance of *D. circinale* in the 16 November assay likely contributed to negative net biomass growth due to unfavourable laboratory conditions. Interestingly, hypolimnetic TN:TP visually corresponde more closely with observed growth responses to nutrient additions than epilimnetic TN:TP during the October to November period (Figure 7).

From mid-December 2020 the lake became increasingly nitrogen limited with strong growth responses to N and N+P treatments which coincided with an extended period where both epilimnetic and hypolimnetic TN:TP was <10 (Figure 7). Chlorophyte species dominated the phytoplankton community during this period with *Dictyosphaerium* sp. the most abundant species (Figure 10). Following the intensive storm event on 31 March 2021 there was a sudden change to weak phosphorus limitation, along with a notable decline in lake chlorophyll *a* in the 9 April assays (Appendix 1). This was followed by a period of co-limitation and by May growth responses began to decline, resulting in no significant difference (*P*<0.05) in chlorophyll *a* and biomass between Day 0 and Day 5 for any of the treatments in the 23 May assay.

Chlorophytes were the dominant taxonomic group during mid to late summer period when the lake was nitrogen limited (Figure 9). Of this group, *Dictyosphaerium* sp. and *Mougeotia* sp. were the most abundant species and remained so until the end of the study. In contrast, diatom biomass was greater during periods of co-limitation in early December and following the heavy rainfall event at the end of March. Diatom abundance was primarily attributable to *Aulacoseira* spp. with *Fragilaria crotonensis* and *Melosira* sp. also present in the May samples. Cyanobacteria community composition was greatest during the *D. circinale* bloom in October and November 2020. In addition to *D. circinale,* the cyanobacterial species *Dolichospermum planctonicum* and *Pseudanabaena mucicola* were present during the

summer N-limitation period but never in great abundance (i.e., <10% of phytoplankton community biomass).

Table 2. Summarised results from 16 nutrient limitation assays conducted fortnightly from October 2020 to May 2021. Results include ratio of total nitrogen to total phosphorus, chlorophyll a concentration, phytoplankton biovolume and net phytoplankton growth. *Indicates a nutrient limitation was indicated but the difference was not statistically significant.

Assay date	Surface mass TN:TP	Mass TN:TP	Chlorophyll *a*	Phytoplankton Biovolume	Net biomass growth
19 October 2020	8.42	Co-limitation	Simultaneous co-limitation	P limitation	P limitation*
1 November 2020	7.33	Co-limitation	Simultaneous co-limitation	Simultaneous co-limitation*	Inconclusive
16 November 2020	21.67	P limitation	Simultaneous co-limitation	Inconclusive	Inconclusive
29 November 2020	10.95	Co-limitation	Serial N limitation	Simultaneous co-limitation	No limitation
13 December 2020	23.85	P limitation	Serial N limitation	Serial N limitation*	No limitation
5 January 2021	7.62	Co-limitation	Serial N limitation	Serial N limitation	N limitation
18 January 2021	8.33	Co-limitation	Serial N limitation	Independent co-limitation	N limitation
2 February 2021	8.80	Co-limitation	Serial N limitation	Serial N limitation	N limitation
14 February 2021	8.75	Co-limitation	Serial N limitation	Serial N limitation	Serial N limitation
1 March 2021	4.33	N limitation	Serial N limitation	N limitation	N limitation
14 March 2021	4.62	N limitation	N limitation	Serial N limitation	Inconclusive
28 March 2021	7.69	Co-limitation	N limitation	N limitation	N limitation
9 April 2021	11.39	Co-limitation	Serial P limitation	P limitation	P limitation*
26 April 2021	6.76	N limitation	N limitation	Simultaneous co-limitation	Simultaneous co-limitation*
9 May 2021	17.10	P limitation	Independent co-limitation*	Independent co-limitation	Independent co-limitation*
23 May 2021	5.93	N limitation	Inconclusive	Inconclusive	P limitation*
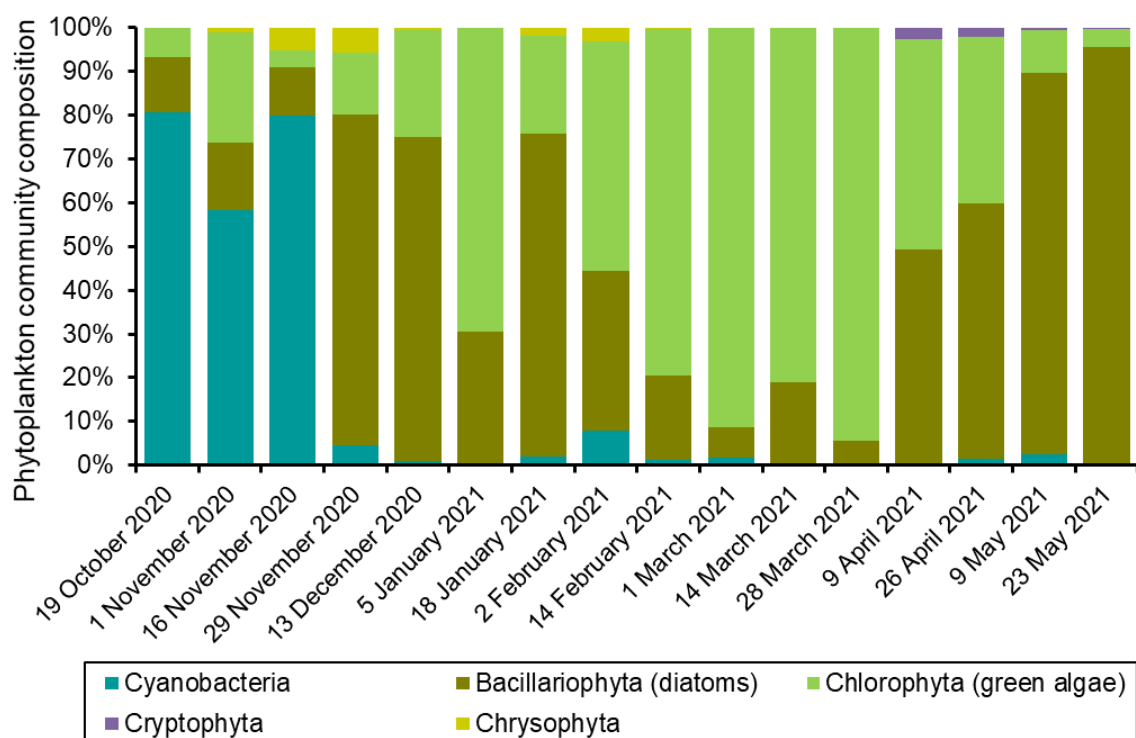
Figure 9. Relative mean phytoplankton community biomass for Lake Rotorua measured at the beginning of each nutrient assay.

Discussion

Following an initial investigation into seasonal nutrient limitation of Lake Rotorua in 2019 by Tempero (2020), the University of Waikato was contracted by the Bay of Plenty Regional Council to undertake a further fine-scale temporal study into changes in phytoplankton nutrient limitation. A total of 16 nutrient limitation assays were conducted at approximately fortnightly intervals from 19 October 2020 to 23 May 2021. The objectives were to determine the limiting macronutrient or macronutrients of the phytoplankton community assemblage and what time-scales variation occurred. This information would then be used to form recommendations as to whether alum dosing rates of inflows to Lake Rotorua could be optimised.

There appeared to be only a weak to moderate visual correlation between lake surface TN:TP and phytoplankton biomass responses to nutrient assays. Total nutrient mass ratios based on annual average nutrient concentrations are more suitable as general indicators of lake nutrient status. This is due to the fact that dissolved nutrient fluxes are more influential to phytoplankton growth at a given point in time, while there is often a lag in TN:TP due to biogeochemical cycling processes and phytoplankton compensatory mechanisms such a P storage and N_2-fixation (Abell et al. 2010, Kolzau et al. 2014). In addition, the use of

laboratory-based assays may not accurately reflect lake ecosystem dynamics, as factors such as zooplankton grazing, micronutrient availability and hydrodynamic mixing may not be representative of lake conditions. During the October to December period, there was a trend away from P limitation towards N limitation, although large fluctuations in TN:TP were indicated in the surface waters during this time period (Figure 7). It is possible that nutrient assay results from this period are more representative of chlorophyte nutrient limitations, as growth responses by the dominant cyanophyte species were limited under the laboratory conditions. Although, the persistence of the *D. circinale* bloom indicates that despite the apparent fluctuations in TN:TP in-lake growth was able to be sustained through physiological compensatory mechanisms or environmental nutrient loading. Intermittent stratification did occur during this period, but hypolimnetic dissolved oxygen was not severely impacted and DRP remained below detection limits, suggesting that the *D. circinale* bloom may have been sustained by external nutrient inputs and decompositional nutrient release from the bloom (DePinto and Verhoff 1977, Østergaard and Skovgaard 1992, Abell and Hamilton 2013). Phytoplankton are capable of taking up both orthophosphate and certain organic P forms (Dyhrman et al. 2006) in excess to their requirements for cell homeostasis and growth (Rhee 1973), which has been designated luxury uptake (Solovchenko et al. 2019). This provides the ability to overcome transient local P depletion, prolonging growth while environmental conditions are favourable. Some filamentous cyanobacterial species such as *Dolichospermum, Aphanizomenon*, *Cylindrospermopsis*, and *Nodularia*, are also capable of fixing inorganic atmospheric N_2 into organic forms (Paerl et al. 2020). However, the enzyme that converts nitrogen gas to ammonia is rapidly and irreversibly destroyed in the presence of oxygen and protection of the enzyme requires production of specialised cells known as heterocysts, which provide suitable anaerobic conditions for N_2 fixation (Adams 2000). There is a significant energetic cost in the production of heterocysts and they must be supplied with photosynthate from nearby vegetative cells as they lack the oxygen generating photosystem II component (Golden and Yoon 2003). Heterocysts were present in the *D. circinale* filaments during the October–November bloom providing the ability for N_2-fixation to sustain growth during periods of low N availability, while luxury P uptake was sufficient to maintain growth through periods of P depletion. This could explain the apparent disconnect between lake TN:TP and phytoplankton biomass responses to nutrient addition.

The *D. circinale* bloom abruptly collapsed towards the end of November to be replaced by the diatom species *Fragilaria crotonensis* and *Aulacoseira* spp. No significant shift in nutrient availability was apparent at this time, with indicators showing either co-limitation or weak N-limitation. This period coincided with stratification breakdown and increased vertical mixing (Figure 4). Cyanobacterial species often prefer warm, still, weather conditions that allow them to remain near the surface where they form dense blooms enhancing their own access to light while shading other phytoplankton species (Reynolds et al. 1983, Huisman et al. 2004). In contrast, diatoms and chlorophytes are more tolerant of vertical mixing and variable

irradiance, allowing them to out-compete cyanobacteria (Litchman 2000). This difference in tolerance to light fluctuations and physical mixing may also explain why cyanophyte growth responses in the nutrient assays were often weak or even declined over the incubation period (i.e., Appendix 1, 16 November) as the constant turbulence supplied by the orbital shakers was not favourable to cyanophyte growth or was more favourable to chlorophytes and diatoms allowing them to out-compete the cyanobacteria.

From mid-December 2020 the lake began to transition to an extended period of N-limitation which ran until the end of March 2021. Strong lake stratification was evident from mid-December until the end of March, although interspersed with brief periods of mixing. Increased DRP and DIN were present in the hypolimnion during February, but this did not translate through to increases in epilimnetic dissolved nutrients. These conditions should have favoured cyanobacteria, and while several species were regularly observed, the group never constituted >10% of phytoplankton community biovolume. Chlorophytes, primarily *Dictyosphaerium* sp., were the dominate group during this period, Sommer (1989) reported that *Dictyosphaerium hotryella* favoured low N:P conditions indicating that cyanobacteria may have been competitively excluded. There was also a trend of increasing TP over this period along with increasing surface chlorophyll *a,* this may have resulted in accumulation of organic P through phytoplankton uptake of DRP release during the brief mixing periods. Similar trends have been observed in other shallow eutrophic lakes which were attributed to increased internal loading due to organic matter mineralization and the release of inorganic P as temperature increased (Sondergaard et al. 2001). Reduced N loading during summer baseflow has previously been observed for serval inflows to Lake Rotorua (Hoare 1982, Me et al. 2018), which may help to explain the extended period of N-limitation.

An intensive rainfall event in the Lake Rotorua catchment occurred on the 31 March 2021. Total 24-h rainfall to midnight on 31 March was 48.4 mm, the magnitude of which was similar to other rainfall events recorded during the study (Figure 5). More than 30 mm of the total rainfall occurred in a 1-2-hour period, resulting in large scale runoff and localised flooding around Rotorua City. Following the storm event, N-limitation rapidly shifted to P-limitation with concurrent increases in both TIN and TN observed in Lake Rotorua. There was also a 'wash-out' effect in the lake as chlorophyll *a* concentration had markedly decreased by the subsequent assay sampling on 9 April (Figure 8). The effect of the rainfall event can also be observed in chlorophyll fluorescence data recorded by a Sonde deployed in Te Ruapeka Bay during the same period (Figure 10) (Tempero and McBride, unpublished report). The decline in chlorophyll *a* can likely be attributed to a dilution effect and the change in environmental conditions causing a collapse in the *Dictyosphaerium* population.
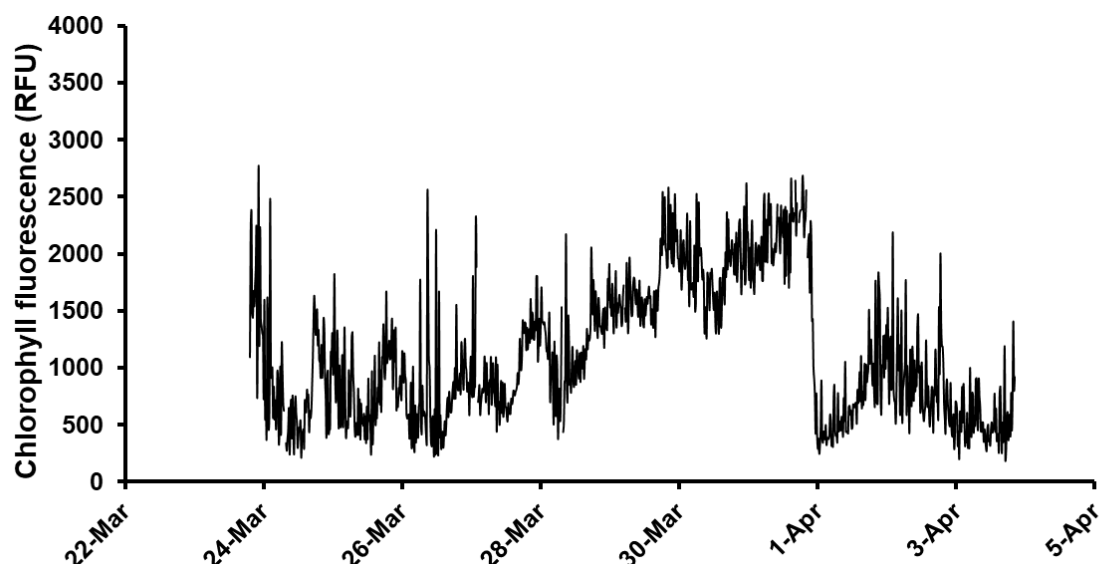
Figure 10. Chlorophyll fluorescence data from a Sonde deployed at 1.5 m depth in Te Ruapeka Bay from 23 March–3 April 2021. The sharp decrease in fluorescence coincides with the intensive rainfall event on the evening of 31 March 2021. Reproduced from Tempero and McBride, unpublished report.

The seasonal fluctuations of N and P availability in the current study appear similar to those described for other temperate limnetic systems by Williamson et al. (2018) and Andersen et al. (2020). Generally, external N and P loading is high in spring and then declines in the summer as inflow discharges decline. During the summer, internal loading becomes more important in polymictic lakes due to repeated internal nutrient cycling from stratification and mixing events. This results in phytoplankton P limitation in the spring, transitioning to N limitation or co-limitation (primary N) in summer, then returning to P/colimitation over the winter due to increased N loading from the catchment from increased inflow (Williamson et al. 2018, Andersen et al. 2020). However, the influence of storm-driven high discharge events on N and P availability in limnetic systems has not been widely reported. Storm events in winter/spring, may reduce TN:TP for short periods of time as stream P increases disproportionately compared to N due to increased mobilisation of particulate P (Williamson et al. 2018, Kelly et al. 2019). Summer storm events, especially following extend periods of little rainfall in agricultural catchments, may increase N:P ratios as DIN stored within the catchment is mobilised (Abell 2013, Abell et al. 2013, Tempero and Hamilton 2014), as was observed in the Rotorua storm event on 31 March 2021, resulting in a rapid, transient shift to P limitation.

The storm event also marked a shift in phytoplankton community composition from dominance by *Dictyosphaerium* sp. (chlorophyta), which increased in relative abundance over the N limitation period, to diatom species such as *Aulacoseira* spp. and *Fragilaria crotonensis.*

Diatoms increased in relative abundance through to the end of the study in May and the lake shifted towards nutrient co-limitation along with conditions which are favourable to diatoms, including increased vertical mixing and cooler temperature (Reynolds et al. 1983, Litchman 2000). The final nutrient assay (23 May) was inconclusive due to poor growth responses across all treatment groups. This was likely due to insufficient photoperiod (10 h day-length), similar poor growth rates occurred for the seasonal winter assay conducted in the previous nutrient limitation study of Lake Rotorua (Tempero 2020).

Implications for alum dosing of Lake Rotorua

Data from phytoplankton nutrient assays conducted from October 2020 to May 2021 indicates that nutrient availably varied both seasonally and in response to stochastic events. During the study period, N limitation and co-limitation were primarily observed with only brief periods on P limitation. Although winter and early spring periods were not assessed, these data indicate that prolonged periods of P limitation do not occur despite the current alum dosing programme. Alum dosing of the Utuhina and Puarenga streams appears to be highly effective, sequestering an estimated 5.38 t DRP y^{-1}, equivalent to 88.2% of the estimated external anthropogenic DRP load to Lake Rotorua (McIntosh 2012, Tempero et al. 2015, Hamill 2021). This is comparatively small fraction (~11%) of the estimated 48.7 t y^{-1} of external TP loading to Lake Rotorua (Tempero et al. 2015). Studies examining the distribution and sediment accumulation of alum derived aluminium in Lake Rotorua have consistently concluded that alum dosing is unlikely to significantly reduce the estimated 36 t y^{-1} internal P loading (c.f. 23.4 t y^{-1} anthropogenic external P load) (BOPRC 2009, Özkundakci et al. 2014, Tempero et al. 2015, Tempero and Hamilton 2016, Tempero 2019, Tempero and Davies-Calway 2021). Özkundakci et al. (2014) determined that the cumulative areal dose rate of aluminium in Lake Rotorua for the years 2007 to 2011 was 7 g Al m^{-2}, which also partially coincided with the peak dosing rate from mid-2010 to mid-2012 (mean 252 kg Al day^{-1}). This areal dose rate was comparatively lower than the 10–70 g Al m^{-2} across 12 Danish and United Sates lakes reported by Egemose et al. (2013) and Huser (2012), respectively. In addition, the areal dose rate reported by Özkundakci et al. (2014) was assumed to be influenced by sediment focusing, the process whereby sedimented alum floc is redistributed from shallower to deeper zones of the lake where much of the internal P loading occurs. However, successive sediment surveys of Lake Rotorua for alum derived aluminium conducted between 2011–21 found aluminium was primarily accumulating in the near-shore environment, well above the Lake Rotorua's hypoxic zone. It has also been theorised that alum floc entering Lake Rotorua from the Puarenga Stream may remained in suspension due to wind-driven wave action and is discharged from the lake before it can sediment to deeper areas of the lake (Tempero 2019). Current alum dosing rates are also significantly lower than the peak rates of 2010-12, from mid-2012 alum dose rates were reduced to ~200 kg Al day^{-1} and then further reduced

to ~100 kg Al day^{-1} in 2018 when dosing of the Puarenga Stream was halted. It should be noted that the resumption of alum dosing to the Puarenga Stream in late November was co-incidental to the decline in *D. circinale* bloom, as the bloom had largely dispersed when dosing restarted on 23 November (Figure 11).
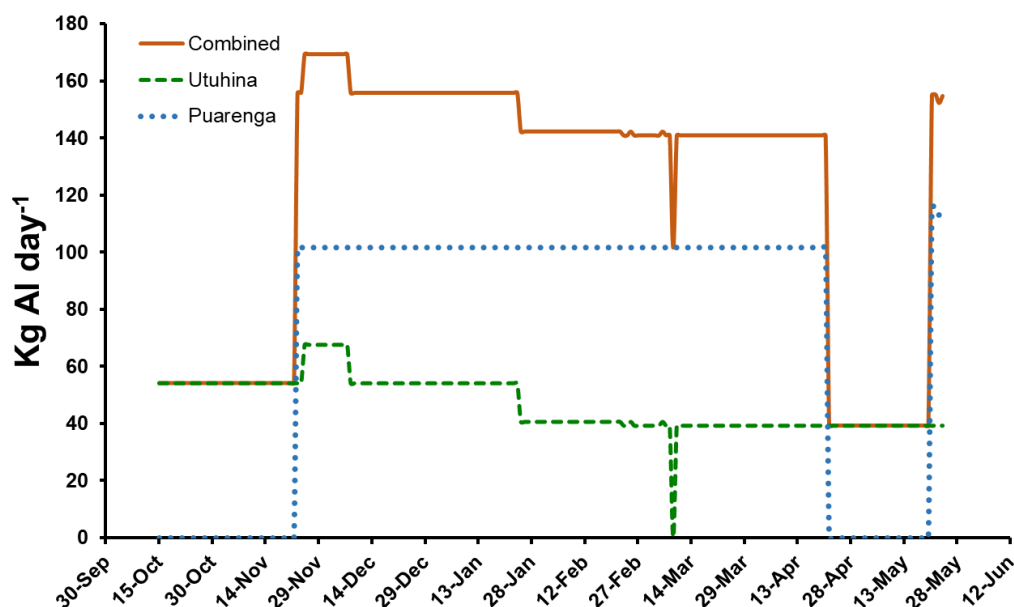

Figure 11. Daily aluminium dose rate to the Utuhina and Puarenga inflows to Lake Rotorua during the nutrient limitation study period 19 October 2020 to 23 May 2021.

Given that Lake Rotorua appears to be primarily N limited or co-limited for much of the year, there appears to be little opportunity for adaptive management of alum dosing to the Puarenga and Utuhina Streams in order to optimise aluminium application. Recent (2013–22) daily dose rates are significantly lower (1–200 kg Al day^{-1}) than the peak rates (>400 kg Al day^{-1}), which were associated with the improvements in lake TLI from 2006–12 (Figure 1). Current alum dose rates, along with improvements in catchment management, appear to have stabilised the lake close to the annual average TLI target of 4.2. Further reductions in internal P loading are unlikely as alum derived aluminium floc is primarily accumulating in the near-shore area near the discharge point of the Utuhina Stream (Tempero and Hamilton 2016, Tempero 2019), limiting the adsorption of P released from deeper in the lake under hypoxic conditions.

This study does not cover the winter and early spring periods that typically experience higher rainfall and external N loading through increased infiltration and surface runoff (Me et al. 2018). Abell and Hamilton (2013) reported that only 25% of particulate P was bioavailable to P limited phytoplankton in August storm event discharges from the Ngongotaha and

Puarenga Streams. Also, despite the potential bioavailability of the particulate P, a laboratory bioassay indicated that, under oxic conditions, suspended sediments acted as a sink rather than a source of bioavailable P to P-limited phytoplankton (Abell and Hamilton 2013). This suggests that while increased N loading occurs during the winter-spring it is unlikely that P limitation will be of sufficient duration to warrant a reduction in alum dosing. Further research into the dynamics of phytoplankton nutrient limitation during the winter and early spring may help to improve understanding of seasonal driving factors in Lake Rotorua.

Conclusions

Fortnightly phytoplankton nutrient limitation assays of Lake Rotorua were conducted from October 2020 to May 2020. Nitrogen limitation was present for most of the summer months (December–March) and nutrient co-limitation during the spring and late autumn. Only short (~2 weeks) periods of P-limitation were observed, one of which was associated with an intensive storm event in the Rotorua catchment at the end of March. Due to the limited periods of P-limitation there appears to be little potential for optimisation of alum dose rates to take advantage of natural periods of P-limitation in Lake Rotorua. While current alum dose rates, in conjunction with improvements in catchment management, appear to have stabilised the lake TLI near the target of 4.2, cyanobacterial blooms are still likely to occur under favourable environmental conditions as the system remains eutrophic.

Recommendations

1. The effectiveness of alum dosing on lake internal P-loading remains an open question. Quantification of lake-wide sediment P release rates would assist in determining whether declines in lake DRP are due to sequestration of P or a natural decline in the sediment P pool from reduced catchment loading.
2. Phosphorus limitation during the winter-early spring may occur and further nutrient limitation assays conducted at sub-monthly intervals would help to determine whether optimisation of alum dosing is possible for this period. Such fine-scale temporal resolution would be required in order to differentiate the effects of environmental perturbance on nutrient availability.
3. Current nutrient monitoring systems do not have the required resolution to provide guidance regarding nutrient availability in Lake Rotorua. In addition, simple TN:TP ratios are not reliable indicators of phytoplankton nutrient requirements. Further investment into the development of environmental forecasting systems such as hydro-dynamic models and real-time nutrient monitoring may provide the temporal

resolution to achieve adaptive management of within the Rotorua alum dosing programme.

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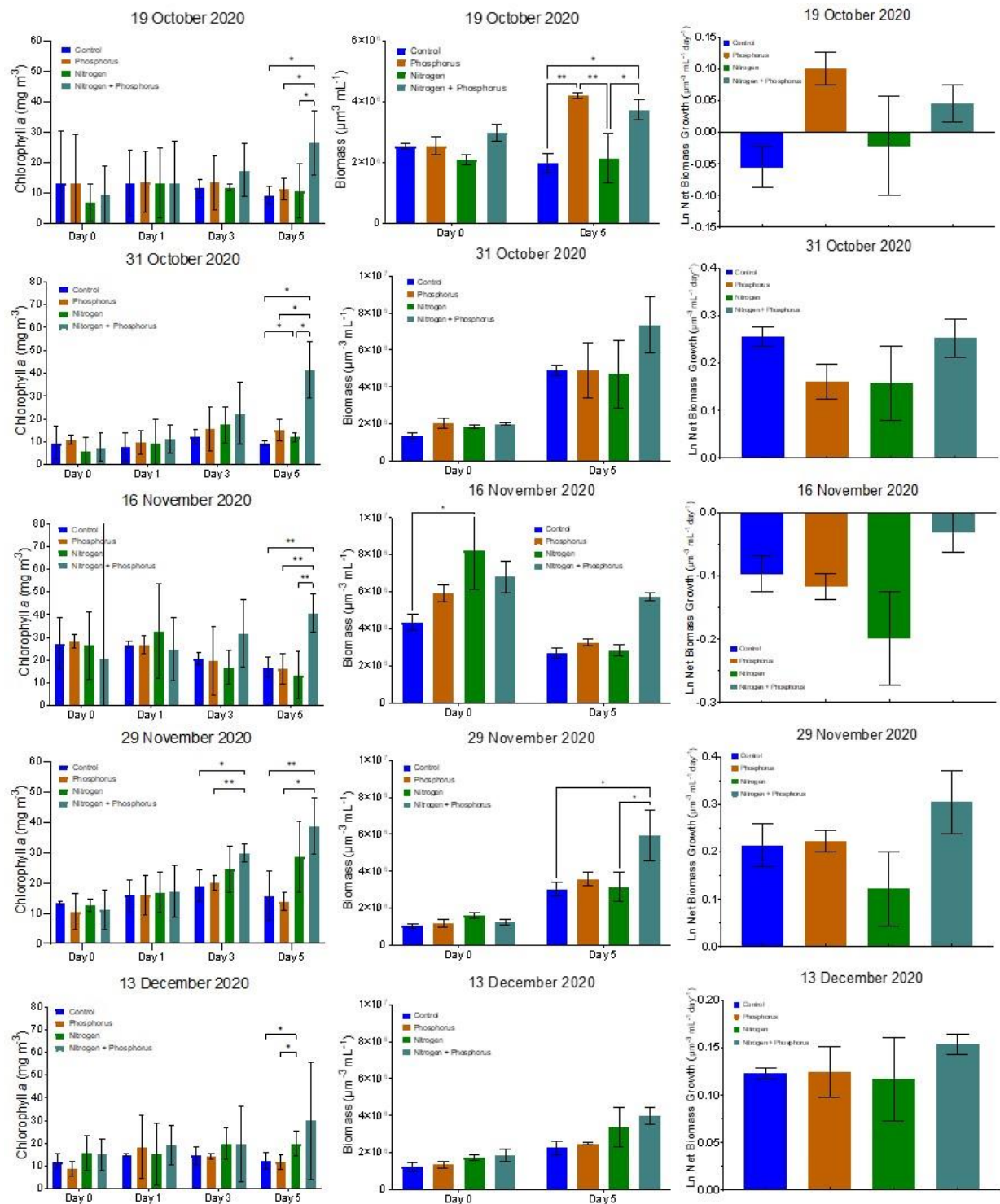
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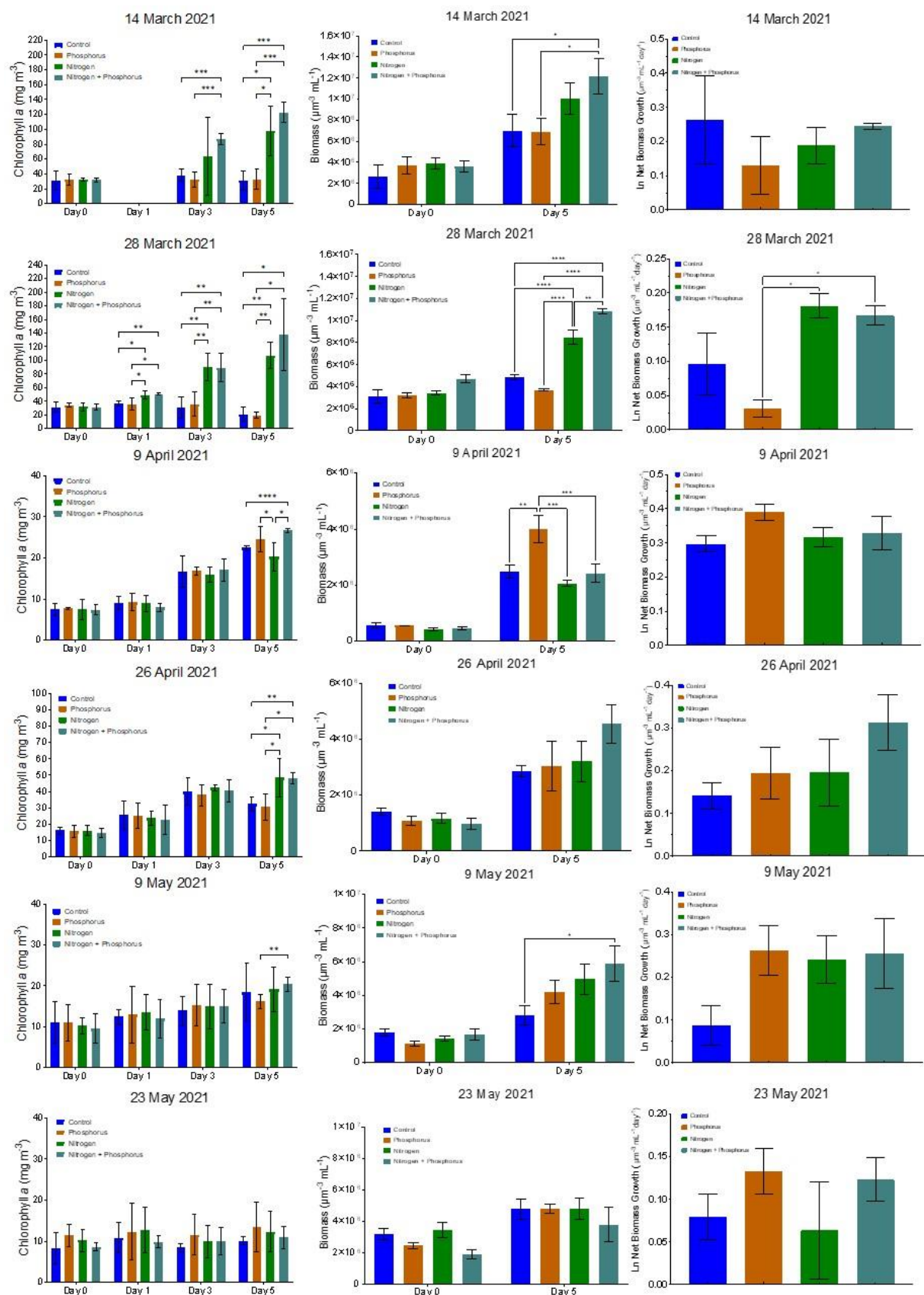
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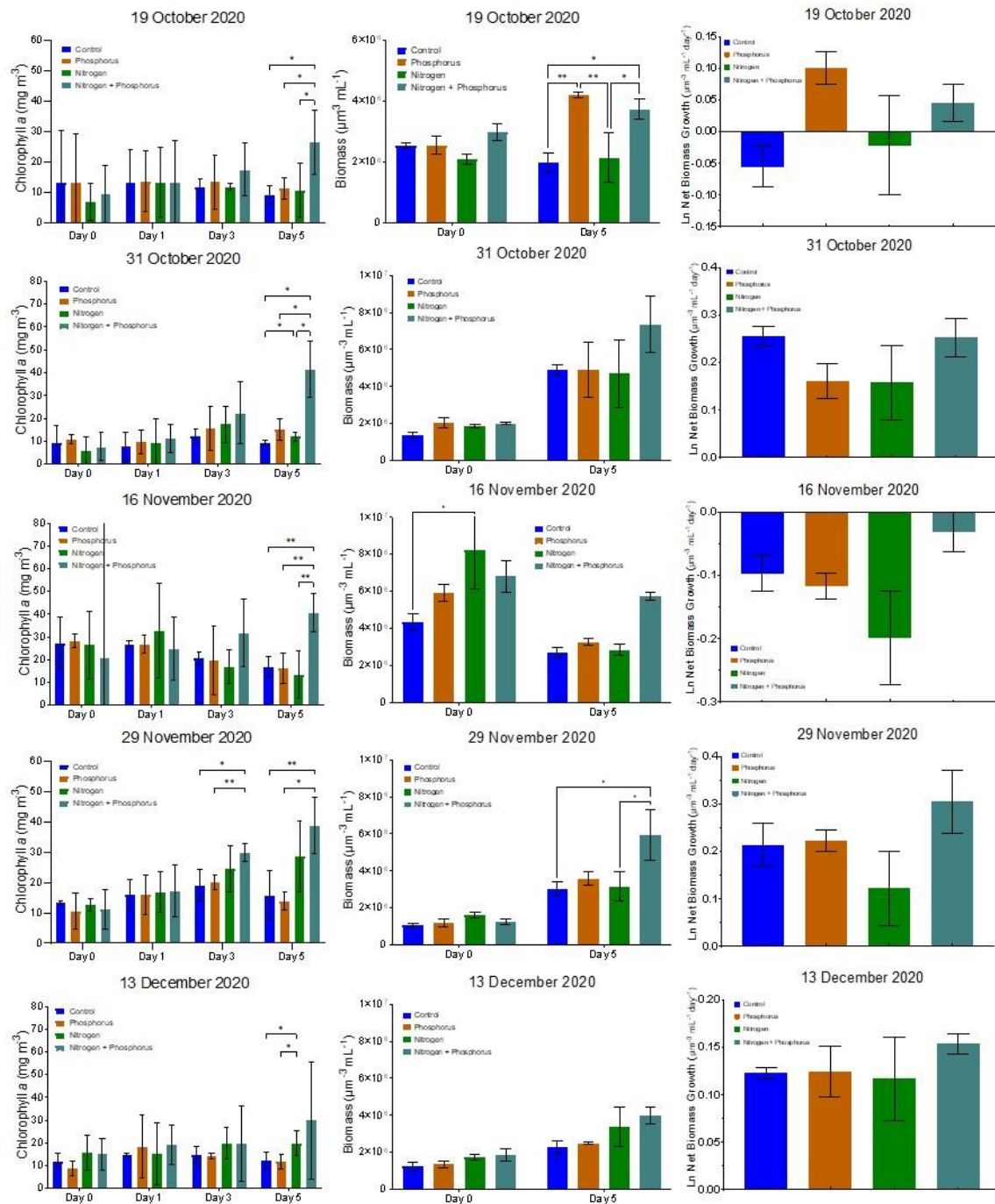
Results of Lake Rotorua nutrient limitation assays. Mean (*n*=3) chlorophyll *a* concentration (left), phytoplankton biomass (centre) and net phytoplankton biomass growth (right) in response to the addition of either phosphorus (10 mg-P m⁻³), nitrogen (100 mg-N m⁻³) or nitrogen + phosphorus (10 mg-P m⁻³, 100 mg-N m⁻³) after 5-days. Error bars indicate Standard Error. Within groups, significantly different (ANOVA <0.05) treatments are indicated by either * (P<0.05), ** (P<0.01) or *** (P<0.001).

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cont'd. Mean (n=3) chlorophyll *a* concentration (left), phytoplankton biomass (centre) and net phytoplankton biomass growth (right) after 5-days.