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Title: Nitrogen and phosphorus limitation of phytoplankton growth in New Zealand lakes: Implications for eutrophication control

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ABSTRACT

We examine macronutrient limitation in New Zealand (NZ) lakes where, contrary to the phosphorus (P) only control paradigm, nitrogen (N) control is widely adopted to alleviate eutrophication. A review of published results of nutrient enrichment experiments showed that N more frequently limited lake productivity than P, however, stoichiometric analysis of a sample of 121 NZ lakes indicates that the majority (52.9%) of lakes have a mean ratio of total nitrogen (TN) to total phosphorus (TP) (by mass) indicative of potential P-limitation (> 15:1) whereas only 14.0% of lakes have mean TN:TP indicative of potential N-limitation (< 7:1). Comparison of TN, TP and chlorophyll *a* data between 121 NZ lakes and 689 lakes in 15 European Union (EU) countries suggests that at the national scale, N has a greater role in determining lake productivity in NZ than in the EU. TN:TP is significantly lower in NZ lakes across all trophic states, a difference that is driven primarily by significantly lower in-lake TN concentrations at low trophic states and significantly higher TP concentrations at higher trophic states. The form of the TN:TP relationship differs between NZ and the EU countries, suggesting that lake nutrient sources and/or loss mechanisms differ between the two regions. Dual control of N and P should be the status quo for lacustrine eutrophication control in New Zealand and more effort is needed to reduce P inputs.

INTRODUCTION

Cultural eutrophication has been identified as the primary problem affecting surface water quality globally (Smith and Schindler 2009). The causal agents of over-enrichment of surface waters with nitrogen (N) and phosphorus (P) produce symptoms that include: enhanced growth of phytoplankton and other aquatic plants; deoxygenation of deeper waters when stratification is present; and a range of adverse impacts to freshwater biota (Carpenter and others 1998). Controls on the input of nutrients that limit phytoplankton growth, in accordance with Liebig's Law of the Minimum (van der Ploeg and others 1999), are therefore integral to controlling eutrophication in freshwaters (Smith and others 1999). Phytoplankton species differ, however, in their nutritional requirements (Sterner and Hessen 1994) and therefore it is simplistic to assume that a single nutrient will always limit the growth of all phytoplankton species in a lake community. It is possible however, to identify the form of the nutrient that limits phytoplankton net primary productivity at the ecosystem scale over a period of weeks to years (Håkanson and others 2007) and it is this aspect of nutrient limitation that is of most interest to lake managers concerned with controlling the undesirable effects of cultural eutrophication.

Phosphorus has been established as the nutrient that commonly limits productivity in lakes (Schindler 1974; OECD 1982). Unlike other macronutrients, P has no gaseous atmospheric cycle and there are no biological mechanisms, comparable to nitrogen-fixation for the N cycle, to redress deficiencies (Schindler 1977). The 'phosphorus limitation paradigm' (Sterner 2008) has been increasingly used to support calls for P-only control to halt and reverse the process of cultural eutrophication. Proponents of P-only control claim that the ability of some species of cyanobacteria to fix di-nitrogen and thus potentially offset N reductions renders N-control to be an unnecessary cost for society

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(Schindler and others 2008; Wang and Wang 2009; Welch 2009). This view has been rebutted, however, by those who support a dual nutrient control strategy due to the propensity for lakes to become limited by N as well as P, (Elser 2007; Lewis and Wurtsbaugh 2008), absence of N_2 fixation in many cyanobacteria (Howarth and others 1988), inability of N_2 fixation to always balance N load reductions (Scott and McCarthy 2010) and the need to consider downstream impacts on marine systems which are typically limited by N (Conley and others 2009; Paerl 2009). If advocates of the P-only control paradigm are correct, then efforts to 'loosen N control' (Wang and Wang 2009) could provide significant savings in pollution abatement and waste-water treatment costs, however, such a relaxation in standards could have severely detrimental effects on lake ecosystem health if applied to situations that differ from the perceived status quo of P-limitation.

The nutrient limitation status of a lake may be inferred from both experimental and observational data. Nutrient enrichment experiments can be undertaken at a range of 'organisational levels' (Hecky and Kilham 1988), and generally involve adding known concentrations of specific nutrient species to lake water samples and measuring the resultant phytoplankton productivity to investigate nutrient limitation in a specific lake system. In such experiments, an individual nutrient is therefore determined to be limiting if its addition results in a significant positive phytoplankton growth response, relative to a control. Alternatively, observations of the ratio of N to P in lake water, in relation to the nutritional requirements of phytoplankton, can be used to infer whether a lake is likely to be limited by N or P or both nutrients (e.g. Smith 1982). A ratio of N:P of 7.2:1 by mass (16:1 by mole) is often used as a benchmark of balanced growth requirements, consistent with the 'elementary composition of plankton' presented by Redfield and others (1963)

and based on data collected by Fleming (1940). Lake water with a significantly lower ratio suggests that the lake is N-limited, while a significantly higher ratio suggests that it is P-limited. The exact ratio at which either nutrient becomes limiting may vary amongst lakes as well as within lakes, depending on the phytoplankton community that is present, and therefore a range of N:P ratios have been proposed to classify the nutrient limitation status of lakes (e.g. see Healey and Hendzel 1979; OECD 1982; Downing and McCauley 1992; Guildford and Hecky 2000).

Eutrophication is a particular issue in New Zealand (NZ) where it is estimated that 30% of lakes greater than 1 ha in area (n > 1000) have very poor to extremely poor water quality as a result of cultural eutrophication (Ministry for the Environment 2007). The prevailing view is that lakes in NZ are comparatively more likely to be limited by N than those in other developed nations based on a study of 27 lakes undertaken by White (1983). A reflection of this is that numerous lakes in NZ such as Lake Taupo and the Te Arawa lakes around Rotorua have nutrient reduction targets in place specifically for the reduction of N (Environment Waikato 2003; Burns and others 2009). Furthermore, the Trophic Level Index, which is used to provide a numerical indicator of the trophic status of lakes in NZ, includes a measure of total N (Burns and others 1999), unlike the Trophic State Index that is used widely in the USA (Carlson 1977) and the fixed boundary system developed by the OECD (1982).

In light of the recent debate about the relative merits of dual N and P control versus P-only control to repress productivity in lakes (Schindler and others 2008; Conley and others 2009; Paerl 2009), and in response to calls for more data on N-limitation (Schindler and Hecky 2009), this study re-examines the prevalence of N- and P-limitation in NZ lakes. The specific objectives of this study are two-fold: (1) to determine the current status of

macronutrient limitation of phytoplankton in NZ lakes by reviewing published literature on nutrient enrichment experiments and analysing nutrient concentrations for a large number of lakes and, (2) to ascertain differences in in-lake macronutrient abundance between lakes in NZ and those in a region of the northern hemisphere (countries in the European Union) where a substantial body of research on this topic has been undertaken.

MATERIALS AND METHODS

Analysis of New Zealand Lakes

Concentrations of total nitrogen (TN), total phosphorus (TP) and chlorophyll a (chl a) for 121 lakes were obtained from 10 of the 16 mainland regional councils in NZ. Northland was disproportionally represented in the sample (40 lakes) and no data were obtained for the eastern North Island (Gisborne and Hawkes Bay) and the north of the South Island (Marlborough and Nelson). The dataset encompasses a broad range of lake types with varying morphological characteristics and trophic status. Samples were collected by regional environmental managers, either from the lake surface, or from integrated depths in the surface mixed layer, at monthly or quarterly intervals during the period of 2004 to 2006. All samples were analysed using standard methods based on APHA (1998) and described in Burns and others (2000). Mass ratios of TN to TP in each lake were used as a stoichiometric indicator of the potential for N- or P-limitation. It was assumed that TN:TP > 15:1 is indicative of potential P-limitation, 15:1 > TN:TP > 7:1 is indicative of potential N- and P co-limitation, and TN:TP < 7:1 is indicative of potential N-limitation, in accordance with the approach taken in other studies of macronutrient limitation in NZ (White 1983; Ministry for the Environment 2007; McDowell and others

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2009). There are several types of co-limitation (see Morris and Lewis 1988); we use the term in a general context to refer to lake ecosystems where the availability of N and P closely matches that required for balanced algal growth and the control of either nutrient will result in an immediate reduction in phytoplankton biomass.

Analysis of Published Data on Nutrient Enrichment Experiments

Literature relating to nutrient enrichment experiments undertaken in NZ lakes was reviewed using the ISI Web of Science tool. Key terms used in the search included: 'New Zealand', 'nutrient limitation', 'phosphorus', 'nitrogen' and 'nutrient enrichment'. The review focused exclusively on studies that involved the addition of either N or P to phytoplankton samples taken from NZ freshwater lakes where the effect of nutrient concentration was the only variable being tested. Reported effects following co-addition of N and P were not recorded as part of this review as such responses can be interpreted in several ways (see Morris and Lewis 1988) and therefore the aggregation and subsequent analysis of such results can yield inconclusive results. All statistically significant growth responses by phytoplankton to nutrient additions were recorded.

Analysis of Northern Hemisphere Lakes

A combined European Union (EU) dataset was compiled for 689 lakes from the European Environment Agency's (EEA) 'Waterbase - Lakes Quality' dataset (European Environment Agency 2009a). This dataset is used for European state of the environment reporting and has information for over 1500 lakes in the 32 EEA member countries. Lake

data for all 27 EU member countries were inspected and a subset was selected from 15 countries, based on lakes for which annual mean TN, TP and chl *a* concentrations were available. Only data for samples collected since January 2000 were considered and data were representative of 1-191 samples per year. Data that had been flagged by EEA "outlier", "logical rule" and "chemical rule" detection (see European Environment Agency 2009b) and data for 14 lakes in Italy with anomalous TP values were omitted from the dataset. Our resulting EU dataset does not contain data from every EU country and not all countries are proportionally represented in the dataset (e.g. lakes in Finland, Italy and Sweden are represented disproportionally frequently in the dataset, accounting for 35%, 22% and 20% of all lakes respectively).

Statistical Analysis

All lakes (NZ and EU) were categorised into five trophic states based on trophic categories of chl *a* concentrations used in the OECD (1982) fixed boundary system (see Table 1). Variance in median TN:TP, TN and TP between NZ and EU lakes in the five OECD trophic state categories was analysed using a non-parametric Mann-Whitney U test. The relationship between $\log_{10}$ chl *a* and both $\log_{10}$ TN and $\log_{10}$ TP was examined by calculating the Pearson's correlation coefficient (r) and the significance of differences between r-values was calculated using the r to Fisher z transformation. The relationship between $\log_{10}$ TN and $\log_{10}$ TP for lakes in NZ and the EU was estimated using robust locally weighted regression analysis (LOWESS) with a smoothing parameter (α) of 0.5. A significance level of $P < 0.05$ was adopted in all tests. All statistical analyses were undertaken using Statistica (Version 8.0; Statsoft, Tulsa, USA).

RESULTS

N- and P-Limitation in New Zealand Lakes

Mean TN and TP concentrations for 121 lakes range from 44.5 - 4248 mg m^{-3} and 1.5 - 440.0 mg m^{-3}, respectively. The ratio of TN to TP varies from as low as 1.3:1 (Lake Ngakeketa South, Northland), indicative of severe N-limitation, to as high as 89.7:1 (Lake Hawdon, Canterbury), indicative of severe P-limitation. Categorising lakes by trophic state and TN:TP (Table 1) shows that the majority of lakes have TN to TP ratios > 15:1 and are therefore potentially P-limited. A total of 33.1% of lakes have mean TN:TP of 7:1 - 15:1 which approximately equates to the ratio required for balanced algal growth or potential co-limitation by N and P. A minority of lakes have a mean TN:TP of < 7:1, indicating potential N-limitation.

Based on TN:TP, ultra-oligotrophic lakes are most likely to be P-limited and no ultra-oligotrophic lakes have mean TN:TP indicative of potential N-limitation. The proportion of lakes that are potentially N-limited is highest for oligotrophic lakes and then declines with increasing trophic state. As trophic state increases, so does the proportion of lakes where TN:TP is indicative of balanced algal growth or potential co-limitation by N and P.

Analysis of Published Results of Macronutrient Enrichment Experiments

The literature review of nutrient enrichment experiments undertaken in NZ lakes identified eight studies that encompassed 17 lakes (Table 2). In total, results were collated for 18

laboratory bioassay experiments and four experiments undertaken using mesocosm enclosures. Experiments have been conducted on more than one occasion for four separate lakes. All experiments used natural phytoplankton assemblages taken from the lake being studied. A range of different measures of productivity were used; these were: net oxygen evolution (Bayer and others 2008; Downs and others 2008), $^{14}CO_2$ fixation rate (Mitchell and Burns 1983; White and others 1985; Lean and others 1987), change in chl *a* concentration (White and Payne 1977, 1978; Lean and others 1987; White and others 1991; Burger and others 2007) and change in phytoplankton cell density (Burger and others 2007). White and others (1985) and Lean and others (1987) augmented their conclusions with physiological assays to measure luxury uptake of orthophosphate and analysis of measured seston N:P ratios while, similarly, White and others (1991) measured orthophosphate and ^{15}N uptake.

A significant positive response in phytoplankton growth was recorded following N addition in 19 (86.4%) out of 22 experiments while a significant positive response was recorded following P addition in 11 (52.4%) out of 21 experiments. Separate studies yielded differing results for three of the four lakes for which more than one separate study has been undertaken (Lakes Hayes, Rotorua and Taupo).

Comparison Between Lakes in New Zealand and the EU

For NZ lakes, Pearson correlation showed that TN provided a better predictor of chl *a* than TP, whereas TP was a better predictor of chl *a* for the EU lake sample (Figure 1). The difference between the two Pearson's correlation coefficients was not significant ($p > 0.05$) for the NZ dataset but was highly significant for the EU dataset ($p < 0.01$).

Ratios of TN to TP are significantly lower for NZ lakes than for EU lakes for all trophic states (Table 3). Median TN:TP is highest in ultra-oligotrophic lakes in both NZ (24.7:1) and the EU (55.3:1) and decreases with increasing trophic state to a minimum of 11:1 and 21.4:1 for hypertrophic lakes in NZ and the EU respectively (Figure 2a). Median TN is significantly higher in ultra-oligotrophic and oligotrophic lakes in the EU compared to those in NZ but there was no significant difference for all other trophic categories (Figure 2b; Table 3). Median TP is significantly lower for ultra-oligotrophic lakes in NZ than in the EU (Figure 1c; Table 3). Median TP is, however, significantly higher in mesotrophic and hypertrophic lakes in NZ compared to those in the EU. Unsurprisingly, median TN and TP increased with increasing trophic state for both NZ and the EU lakes, with the exception of median TN in EU lakes which is lower in oligotrophic lakes than in ultra-oligotrophic lakes (Figures 1b and 1c).

The form of the relationship between TN and TP differs between the NZ and EU lakes (Figure 3). According to the trajectory of the LOWESS curve, for EU lakes, the rate of increase in TN is greatest towards the centre of the TP range whereas for the NZ lakes, the rate of increase is greatest at the lower and higher ends of the trophic status continuum. Comparison of the gradient of the regression lines indicates that TN appears to increase at a greater rate (relative to TP) in the NZ lakes than in the EU lakes.

DISCUSSION

The objectives of this study were to determine the nutrient limitation status of NZ lakes and to compare in-lake N and P abundance in NZ with that of countries in the EU. We show that phytoplankton growth can be limited by N or P, or co-limited by both nutrients

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in NZ lakes, based on analysis of the findings of published nutrient experiments and analysis of in-lake annual mean TN:TP. Furthermore, the relative likelihood of potential limitation by either N or P varies according to trophic state. Comparison of NZ and EU lakes shows that mean TN:TP is significantly lower in NZ than in the EU, implying that N is likely to have a greater role in controlling phytoplankton growth in lakes in NZ than in the EU. Both TN and TP correlate similarly with chl *a* in NZ lakes, whereas in EU lakes, TP is significantly better correlated than TN with chl *a*. Total N is generally lower in NZ lakes with a low trophic state compared with the EU, while TP is higher in NZ lakes of high trophic state compared with the EU. Overall, the form of the relationship between in-lake TN and TP differs between NZ and the EU.

N- and P-Limitation in New Zealand Lakes

There may be several explanations for the variation between the results obtained from nutrient enrichment experiments and those from analysis of in-lake nutrient concentrations. One possible reason relates to the time-frame encompassed by the two methods; the measurement of short-term phytoplankton response to nutrient enrichment experiments provides a 'snapshot' of the nutrient limitation status of a phytoplankton community at one time (Downs and others 2008) whereas annual mean nutrient ratios provide an indication of the relative abundance of nutrients over longer timescales. As TN:TP can display high intra-annual variation (Barica 1990), the nutrient limitation status of phytoplankton inferred from the results of nutrient enrichment experiments may differ from that inferred from analysis of nutrient stoichiometry depending on the timing of the experiments.

Variation between the results of nutrient enrichment experiments and analysis of nutrient stoichiometry could also be due to shortcomings associated with the two methods. All nutrient enrichment experiments undertaken in NZ have been at the sub-ecosystem level (i.e. not at the whole lake scale) and therefore they may not be directly applicable to the whole lake scale due to the occurrence of temporal and spatial distortions associated with laboratory bioassays (Droop 1977; White and others 1985) and mesocosms (Schindler 1998). Nevertheless, sub-ecosystem scale enrichment experiments are widely used to ascertain the limiting nutrient in lakes (e.g. Guildford and others 2003; Elser and others 2009a) and the analysis of the results of a number of these experiments is an established tool for characterising the macronutrient limitation status of a particular type of system (Moss and others 2004; Elser 2007).

Likewise, the approach taken of comparing TN:TP to the established thresholds of 7:1 and 15:1, representing potential N- and P-limitation respectively, can also be regarded as not definitive. Ratios may vary from lake to lake depending on phytoplankton assemblages as well as their nutritional and physiological status (Sterner and Hessen 1994) and consequently, a range of thresholds in mass TN:TP ratios have been defined to represent respective N- and P-limitation. These include < 13:1 and > 36:1 (OECD 1982), < 9:1 and > 23:1 (Guildford and Hecky 2000) and < 22:1 as an indicator of N-limitation, based on observations of cyanobacteria (potential N-fixers) dominance (Smith and others 1995).

This study has used TN:TP ratios that are consistent with other studies of nutrient limitation in NZ freshwaters and, while there may be a degree of uncertainty associated with defining which nutrient is limiting in lakes where TN:TP is close to that required for balanced algal growth, the existence of both extremely low (1.3:1) and high (89.7:1)

TN:TP ratios supports the conclusion that both N- and P-limitation is a feature of lakes in NZ. While it has been argued that only long-term nutrient enrichment experiments undertaken at the ecosystem scale can provide definitive conclusions about the status of nutrient limitation in a whole lake (Schindler and Hecky 2009), such experiments are only rarely feasible and by their nature they are counterproductive to eutrophication control efforts, at least in the short term.

Comparison of TN:TP Between Lakes in New Zealand and the EU

Atmospheric deposition of N has been found to influence nutrient concentrations in lakes in the Northern Hemisphere (Hessen and others 2009). Variation in atmospheric N deposition rates could therefore account for the significantly lower TN in unproductive (ultra-oligotrophic and oligotrophic) lakes in NZ compared to those in the EU, as has previously been suggested (White 1983). Data for N deposition in NZ are limited, however Parfitt and others (2006) proposed that 1.5 kg N ha^{-1} yr^{-1} is an appropriate value for wet deposition in NZ, which is markedly lower than the average wet deposition N flux for Europe (6.76 kg N ha^{-1} yr^{-1} of NO_3 and NH_4) estimated by Holland and others (2005). Interestingly, despite low TN concentrations for NZ lakes of low trophic state, we found these lakes to be mostly P-limited, based on TN:TP. This is surprising given that atmospheric N deposition rates < 4.5 kg N ha^{-1} yr^{-1} have been shown to promote N-limitation in unproductive lakes in Norway and Sweden (Elser and others 2009a) and rates < 2 kg N ha^{-1} yr^{-1} have been associated with N-limited lakes in Colorado (Elser and others 2009b). This difference may be because TP is relatively more abundant in these systems,

compared to systems of similar trophic state in NZ, as TP is also significantly lower in ultra-oligotrophic lakes in NZ compared with the EU.

Although TN is significantly lower in NZ lakes than in EU lakes at low trophic status, there is no significant difference between TN concentrations at higher trophic status (mesotrophic, eutrophic and hypertrophic). This suggests that total N inputs to NZ lakes are commensurate with those in the EU for lakes with catchments that have been modified by human activities. Nitrogen inputs to NZ landscapes are dominated by agricultural sources (Parfitt and others 2006) which are a major contributor to N pollution in downstream waters and have increased substantially in recent years (Hamilton 2005; Heggie and Savage 2009). It is likely therefore that N from agricultural sources, including urea fertiliser and indirectly via livestock urine, is responsible for the increase in TN concentrations with increasing trophic status in many NZ lakes.

Total phosphorus, like TN, is significantly lower in ultra-oligotrophic lakes in New NZ than in those of the EU. Although P from geological sources has been shown to be relatively high in some parts of NZ (Timperley 1983), this result suggests that in general, at a national scale, P from natural sources is not unusually high, at least compared with the EU. The finding that NZ lakes with higher trophic status (mesotrophic and hypertrophic), have significantly higher TP than those in the EU indicates that P inputs from anthropogenic sources may be particularly high in NZ. As with N, P inputs to NZ landscapes are also dominated by agricultural sources (Parfitt and others 2008) and are increasing with agricultural intensification; for instance, application of 'super-phosphate' fertiliser increased by 60% between 1981 and 2007 (Statistics New Zealand 2008). Urban development in lake catchments is relatively low in NZ compared with other developed

countries (White 1983) and therefore, it is likely that high TP concentrations in productive lakes are predominantly associated with agricultural activities.

The differences in the form of the TN:TP relationship between the two geographic regions suggest that nutrient sources and/or loss mechanisms in NZ are, to a degree, different from those in the EU. The general form of the relationship between TN and TP in the EU lakes closely resembles the one identified by Downing and McCauley (1992), using data from 221 lakes in 14 countries. These authors showed TN:TP to decline in a curvilinear fashion with increased TP, and, attain a minimum and maximum value along the curve trajectory. The authors attributed the first inflection point (the minimum value) to the difference in TN:TP of nutrient export from catchments of oligotrophic lakes and those of meso- and eutrophic lakes while the maximum value was attributed to increased rates of de-nitrification in eutrophic lakes. Based on our analysis, we can only speculate about the possible causes for the differences in the overall N:P relationships. One potential explanation for the steeper gradient of the N:P relationship in NZ lakes is that a relatively low dominance of urban-related nutrient sources, typically characterised by low N:P (Downing and McCauley 1992), results in a higher overall N:P of nutrient sources to lakes in NZ compared to the EU. Other explanations are possible, however (e.g. variation in de-nitrification rates; see Seitzinger and others 2006), and further research into how factors such as these affect in-lake nutrient concentrations could aid understanding of how nutrient cycling processes vary over large spatial scales.

The relationship between TN, TP and trophic state fails to support the prevailing view that N-limitation occurs more frequently in lakes in NZ than in other developed countries, due in part to variation in the natural abundance of N and P (e.g. White 1983). If true, this would imply that the ratio of TN to TP should be low in lakes with low

productivity. Conversely however, we found TN:TP in lakes of lower trophic status is frequently in the P-limited range (> 15:1), suggesting that N-limitation cannot be attributed to a naturally low abundance of N. Nitrogen limitation in NZ lakes, inferred from mean TN:TP, is most frequently associated with productive lakes where P concentrations are very high; ergo, in the majority of cases, N-limitation in NZ lakes is a product of excessive P inputs as opposed to a scarcity of N.

Implications for Lake Management and Eutrophication Control

New Zealand's island status means that the linkages between freshwater and marine systems are frequently short and direct. There is therefore high potential for adverse downstream impacts on marine systems if nutrient pollution in freshwaters is not adequately addressed. In this respect, the control of N, in addition to P, is particularly important as marine systems have been shown to be predominantly N-limited (Elser and others 2007). A number of harmful algal blooms have occurred in recent years in NZ's coastal waters and although these have not been directly linked to excessive N or P from freshwater sources, they have been associated with elevated nutrient regimes (Chang and others 2008). Continued increase in nutrient pollution in freshwaters could therefore cause such blooms to become a more frequent occurrence and nitrogen inputs to freshwater ecosystems should therefore be carefully managed, a line of reasoning that is consistent with that of Paerl (2009).

Analysis of long-term mean nutrient concentrations in this study suggests that although N-limitation is likely to occur in NZ lakes, it is the exception and not the rule. This finding, in addition to the occurrence of very high TP concentrations in productive

lakes in NZ, suggests that more needs to be done to reduce P concentrations, particularly from agricultural activities which are the major source of P loads to New Zealand catchments (Parfitt and others 2008). A variety of improvements to farming and agricultural land management practices can be made to reduce diffuse P loss (Cherry and others 2008) and a study specific to NZ has shown that TP in receiving waters can be reduced by up to 32% over several years as a result of the adoption of such practices (Wilcock and others 2009). Such modifications may not be sufficient, however, in the catchments of the most eutrophied lakes and in these cases, engineering based in-lake rehabilitation measures (Özkundakci and others 2010) and/or a firm commitment to land use change may be required (Edgar 2009).

CONCLUSION

The dual control of both N and P has a role in the management of lakes in NZ to reduce the symptoms of cultural eutrophication as it has been shown that both N and P can potentially limit the growth of phytoplankton. A policy of P-only control, as some studies have advocated (e.g. Schindler and others 2008; Wang and Wang 2009; Welch 2009), should therefore not be adopted as standard practice for eutrophication control in NZ, especially given the high connectivity of freshwater ecosystems with estuaries and the coastal marine environment. Nevertheless, while N-control has a role, more effort should be directed towards controlling P loads to NZ lakes, as P concentrations are significantly higher than those of mesotrophic and hypertrophic lakes in the EU. This study has shown that the relationship between TN and TP in NZ lakes differs from that of other lake systems that have been studied and as such, further research is required to understand how

nutrient sources, in-lake processes and nutrient loss mechanisms interact to influence nutrient concentrations in lesser studied freshwater ecosystems like NZ lakes.

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Table 1. Potential macronutrient limitation status of 121 New Zealand lakes, as inferred from the mean ratio of total nitrogen (TN) to total phosphorus (TP). Trophic state was determined using the categories of mean chlorophyll *a* (chl *a*) concentration used in the OECD (1982) fixed boundary system.

Table 2. Summary of macronutrient enrichment experiments undertaken for New Zealand lakes. A dash indicates that the relevant enrichment experiment was not included in the study.

Table 3. Summary of statistical output of a Mann-Whitney U test of the difference in median total nitrogen (TN), total phosphorus (TP) and TN:TP between lakes in New Zealand (NZ) and the European Union (EU) corresponding to five trophic states (OECD 1982; see Table 1).

Table 1.

Lake trophic status	Mean chl *a* (mg m^{-3})	n	TN:TP < 7:1 (indicative of N-limitation)	7:1 < TN:TP < 15:1 (indicative of N and P co-limitation)	TN:TP > 15:1 (indicative of P-limitation)
Ultra-oligotrophic	≤ 1.0	19	0.0%	10.5%	89.5%
Oligotrophic	1.0 – 2.5	27	22.2%	14.8%	63.0%
Mesotrophic	2.5 – 8.0	37	18.9%	27.0%	54.1%
Eutrophic	8.0 – 25.0	17	11.8%	41.2%	47.1%
Hypertrophic	≥ 25.0	21	9.5%	81.0%	9.5%

Table 2.

Lake	Region	Experiment organization level	Significant response? +N	+P	Incubation period	Study
Hayes	Otago	Laboratory bioassays	No	No	18 h, 24 h	(Bayer and others 2008)
		In-situ mesocosm (2.25 L sub –surface bottles)	Yes	No	5 d	(Mitchell and Burns 1981)
Horowhenua	Manawatu-Wanganui	Laboratory bioassays	Yes	Yes	4 h, 4 d	(White and others 1991)
Johnson	Otago	In-situ mesocosm (2.25 L sub –surface bottles)	Yes	-	5 d	(Mitchell and Burns 1981)
Mahinerangi	Otago	Laboratory bioassays	Yes	Yes	24 h	(Downs and others 2008)
Okareka	Bay of Plenty	Laboratory bioassays	Yes	Yes	2 h, 24 h	(White and others 1985)
Okaro	Bay of Plenty	Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
		In-situ mesocosm (960 L plastic enclosure)	Yes	No	10 d	(Lean and others 1987)
Okataina	Bay of Plenty	Laboratory bioassays	No	Yes	2 h, 24 h	(White and others 1985)
Rerewhak-aaitu	Bay of Plenty	Laboratory bioassays	Yes	Yes	2 h, 24 h	(White and others 1985)
Rotoehu	Bay of Plenty	Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
Rotoiti	Bay of Plenty	Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
Rotoma	Bay of Plenty	Laboratory bioassays	Yes	Yes	2 h, 24 h	(White and others 1985)
Rotomahana	Bay of Plenty	Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
Rotorua	Bay of Plenty	Laboratory bioassays	Yes	Yes	5 d	(White 1978)
		Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
		In-situ mesocosm (3 L plastic container)	Yes	Yes	4 d, 6 d	(Burger and others 2007)
Tarawera	Bay of Plenty	Laboratory bioassays	Yes	No	2 h, 24 h	(White and others 1985)
Taupo	Waikato	Laboratory bioassays	Yes	Yes	5 d	(White and Payne 1977)
		Laboratory bioassays	No	No	2 h, 24 h	(White and others 1985)
Tikitapu	Bay of Plenty	Laboratory bioassays	Yes	Yes	2 h, 24 h	(White and others 1985)

| Waihola | Otago | Laboratory bioassays | Yes | Yes | 24 h | (Downs and others 2008) |

Table 3.

| Trophic State	Variable	n (EU)	n (NZ)	U	Z	p
Ultraoligotrophic	TN	42	19	62	5.241	<0.001
	TP	42	19	192	3.216	<0.05
	TN:TP	42	19	163	3.668	<0.001
Oligotrophic	TN	104	27	519	5.033	<0.001
	TP	104	27	1360	0.248	0.805
	TN:TP	104	27	436	5.505	<0.001
Mesotrophic	TN	297	37	5082	0.744	0.457
	TP	297	37	2443	-5.508	<0.001
	TN:TP	297	37	1674	6.897	<0.001
Eutrophic	TN	170	17	1233	0.994	0.320
	TP	170	17	1156	-1.356	0.175
	TN:TP	170	17	896	2.578	<0.05
Hypertrophic	TN	76	21	634	-1.432	0.152
	TP	76	21	321	-4.174	<0.001
	TN:TP	76	21	242	4.866	<0.001
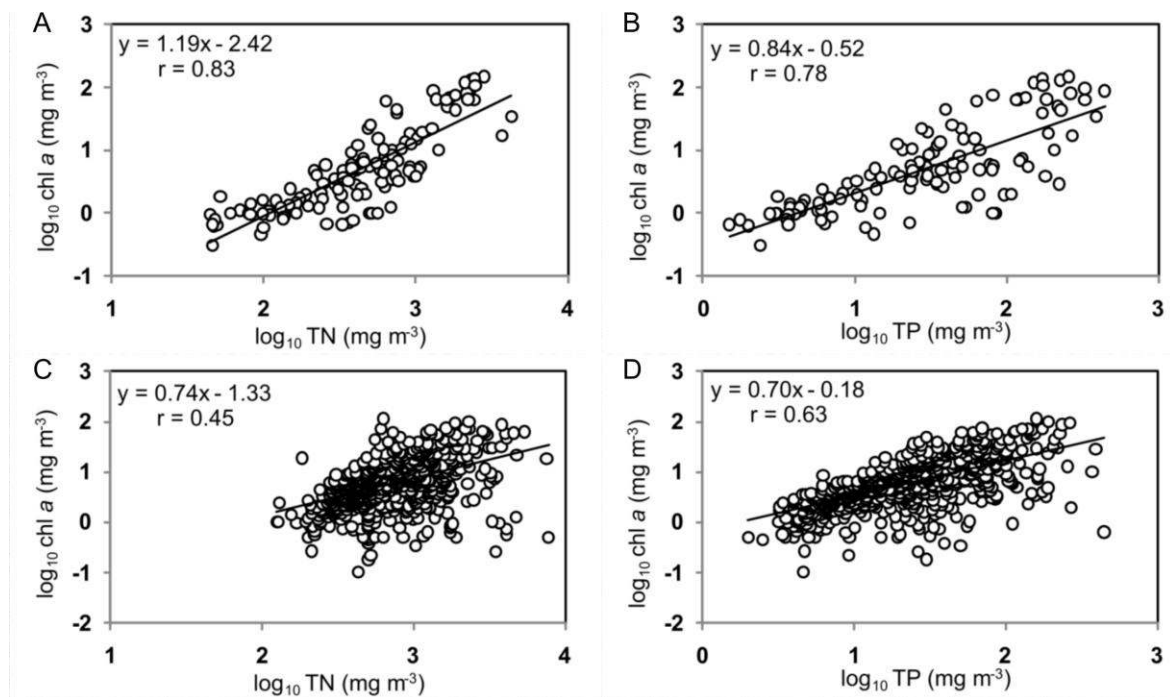
Figure 1. Scatter plots of chlorophyll *a* (chl *a*) concentration against mean total nitrogen (TN) and total phosphorus (TP) concentrations for 121 lakes in New Zealand (A, B) and 689 lakes in European Union countries (C, D). Data are $\log_{10}$ transformed and all correlations are highly significant (P < 0.01).
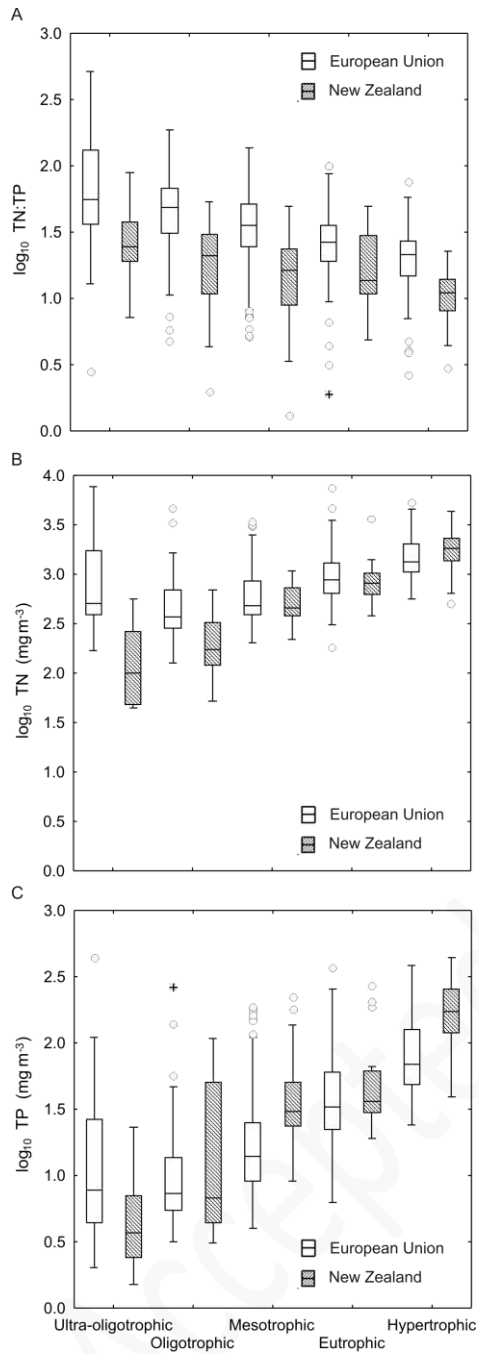
Figure 2. Median mass ratios of total nitrogen (TN) to total phosphorus (TP) (A), TN (B), and TP (C) for 121 New Zealand lakes and 689 lakes in European Union countries, by five categories of trophic status (Table 1). Data are log_{10} transformed. The whiskers represent the non-outlier range, the outer edges of the boxes represent the 25th and 75th percentiles, the lines within the boxes represent the median, circles represent outliers, and crosses represent extreme data points.
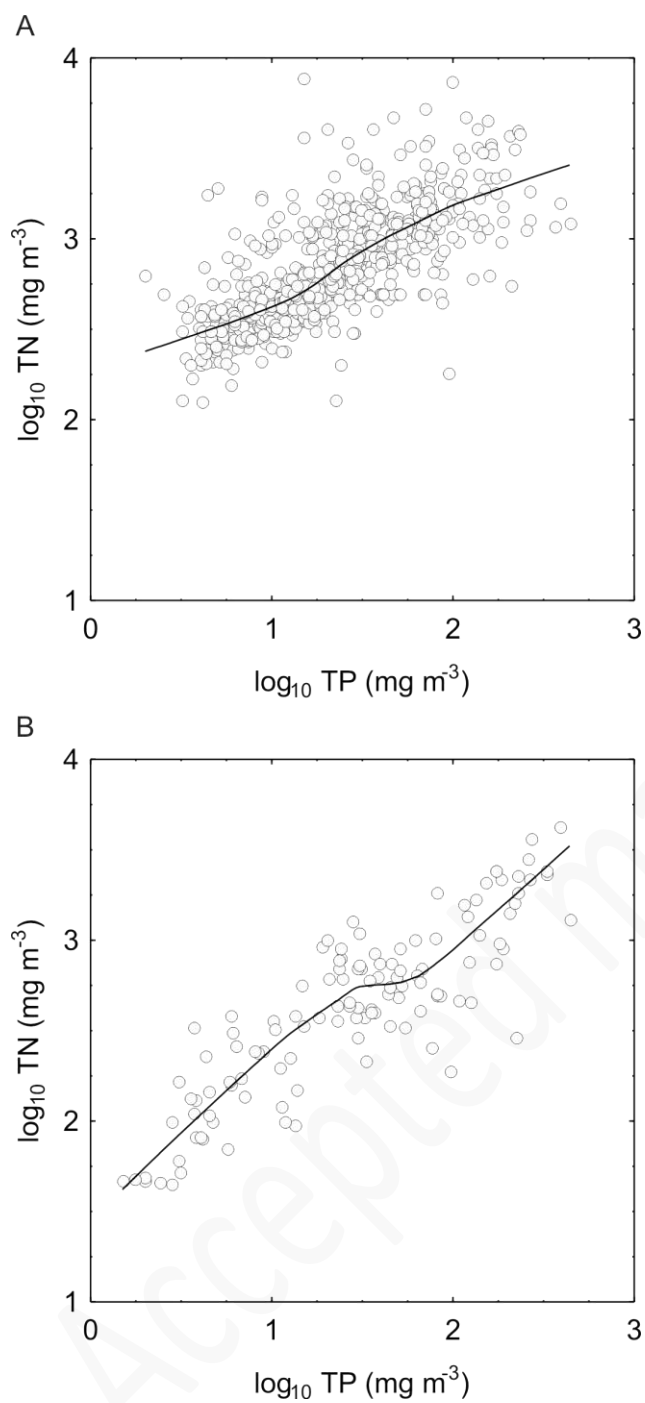
Figure 3. Relationship between total nitrogen (TN) and total phosphorus (TP) (log10 transformed) for 121 lakes in New Zealand (A) and 689 lakes in European Union countries (B). The average trend in the data (solid line) is shown by a LOWESS fitted curve.