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The reduction of macronutrients to levels that limit primary production is often a critical element of mitigating eutrophication and reducing the potential for algal blooms. Lake Okaro has remained highly eutrophic despite an intensive catchment and in-lake restoration programme, including implementation of a constructed wetland, riparian protection, an alum application and application of a modified zeolite mineral (Z2G1) to reduce internal nutrient loading. A one-dimensional process-based ecosystem model (DYRESM-CAEDYM) was used in this study to investigate the need for further nutrient loading reductions of both nitrogen (N) and phosphorus (P). The model was calibrated against field data for a 2-year period and validated over two separate 1-year periods. Model simulations suggest that the trophic status of the lake, measured quantitatively with the Trophic Level Index (TLI), could shift from highly eutrophic to mesotrophic with external and internal loads of both N and P reduced by 75–90%. The magnitude of the nutrient load reductions is indicative of a major challenge in being able to effect transitions across trophic state categories for eutrophic lakes.

Keywords: Lake Okaro; lake restoration; nutrient limitation; DYRESM-CAEDYM; model validation; phosphorus; nitrogen

Introduction

Control of diffuse and point sources of phosphorus (P) and nitrogen (N) remains a global challenge (Schindler 2006; Carpenter 2008; Conley et al. 2009) despite more than 50 years since the recognition that these nutrients are critical for primary production in aquatic ecosystems. While net phytoplankton growth can be constrained by factors other than nutrients (e.g. light and grazing), there is continued recognition of the critical role of P in the eutrophication process (OECD 1982; Schindler et al. 2008), although many lake restoration efforts focused predominantly on P control have fallen short of expectations (Conley et al. 2009). Similarly, in management

focused predominantly on N there is risk of enhanced growth of N-fixing cyanobacteria that may negate the effectiveness of this control strategy (Schindler et al. 2008). Lewis & Wurtsbaugh (2008) proposed a N + P control paradigm, which emerged from evidence of co-limitation of N and P for phytoplankton growth across a large number of inland waters.

Numerical models of aquatic ecosystems that couple physics and biogeochemistry (e.g. Kamykowski et al. 1994; Schladow & Hamilton 1997) are valuable tools in aquatic ecosystem research. They have been used for examining theoretical aspects of ecosystem behaviour, which may be unattainable by other means (Franks 1995) and the interactions between

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trophic dynamics and, for example, climate variability (Norberg & DeAngelis 1997). These models have been used for forecasting purposes and as environmental management decision support tools, particularly for the control of eutrophication (Friedman et al. 1984; Burger et al. 2007a; Trolle et al. 2008). They have also been used in combination with water quality indices to collate the detailed temporal and spatial information on model output variables into numerical rating values (Gal et al. 2009). There are widely used water quality indices directly related to eutrophication assessment such as the Trophic Level Index (TLI; Burns et al. 1997) and Trophic State Index (Carlson 1977), but we are not aware of any applications of these indices for interpreting the outcomes for different scenarios simulated with numerical water quality models.

The decline over the past 30–40 years of water quality in the Te Arawa (Rotorua) lakes and in New Zealand lakes generally has been linked to increasing nutrient loads from land development for agriculture and greater use of artificial fertilisers (Parliamentary Commissioner for the Environment 2004; Hamilton 2005). Steps are beginning to be taken to redress the decline in water quality, including changing land use around some lakes (Quinn 2009). Amongst the Te Arawa lakes, there has been an intensive restoration programme in Lake Okaro, the focal lake in this study, which commenced in 2003. The TLI is used as the cornerstone by which to gauge the effect of action plans developed to improve water quality of this lake and other Te Arawa lakes. Water quality targets based on the TLI are derived from annual mean surface water concentrations of chlorophyll *a* (chl *a*), total nitrogen (TN), total phosphorus (TP) and Secchi depth (SD). Despite a series of actions implemented at Lake Okaro, including an alum application (Paul et al. 2008), a constructed wetland (Tanner et al. 2007) and most recently a sediment capping application using an aluminium-modified zeolite mineral (Z2G1),

the TLI has remained within the highly eutrophic range (Özkundakci et al. 2010). These restoration methods were collectively designed to reduce both N and P loading to the lake, but were mostly directed towards reducing P loads. The objective of this study was to investigate the need for further nutrient loading reductions of both of both N and P from both external and internal sources that would be required to reduce nutrient and chl *a* concentrations and improve the trophic state of Lake Okaro. We used a dynamic numerical model and multi-year simulations to investigate the response of the lake to different N and P loading rates. We also examined the likely response of reduced water column N and P on the duration and severity of nutrient limitation in phytoplankton, using specific outputs of nutrient limitation status from the model.

Methods

Study site

Lake Okaro (Fig. 1) is a small lake (area 0.32 km^2) of moderate depth (max. depth 18 m), in the Rotorua district on the Central Volcanic Plateau of North Island, New Zealand. The lake is the most eutrophic of the Te Arawa lakes (Paul et al. 2008). It is a monomictic lake and stratifies for around 8 months during summer when there are substantial sediment nutrient releases (Environment Bay of Plenty 2006; Özkundakci et al. 2010). The Regional Water and Land Plan for Bay of Plenty has set a TLI target reduction from the current value of 5.5, which categorises the lake as supertrophic (3-year average to June 2004) to a value of 5.0 (Environment Bay of Plenty 2006). This value does not represent a shift of the trophic status of the lake from its current eutrophic category but the TLI value would be lower than annual values observed since 1992, when continuous monitoring of Lake Okaro commenced by the regional council (Environment Bay of Plenty 2006).
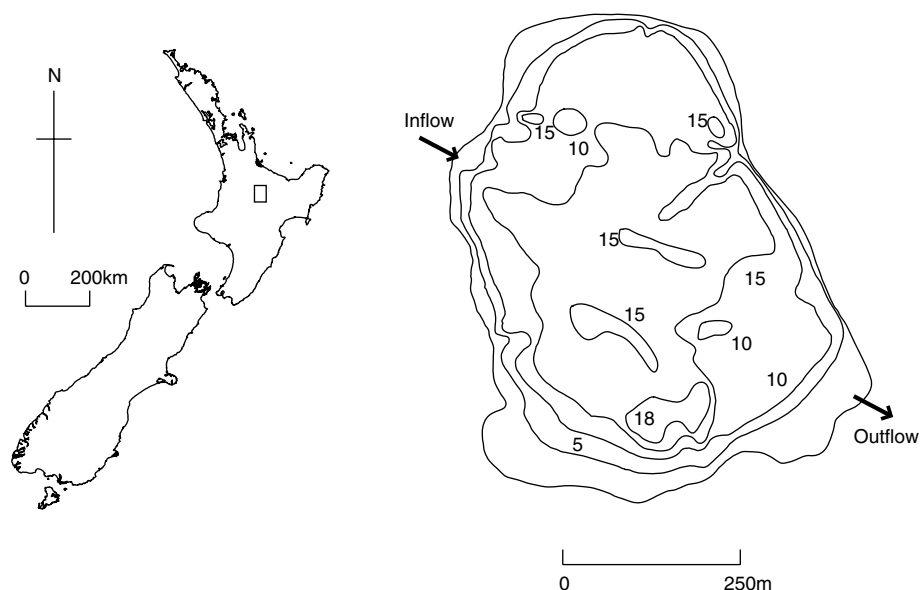
Figure 1 Location map of Lake Okaro showing depth contours of 5, 10, 15 and 18 m (after Irwin 1974).

To improve the water quality of Lake Okaro, Environment Bay of Plenty has set nutrient reduction targets over the long term (15–20 years) and medium term (4–15 years) corresponding to, respectively, external and internal loading reductions of N and P (Environment Bay of Plenty 2006). Intensive catchment and in-lake restoration has been carried out at Lake Okaro to reduce both external and internal nutrient loading. Two permanent stream inflows were diverted into a 2.3-ha surface–flow constructed wetland in February 2006 (Tanner et al. 2007). Riparian protection works were undertaken progressively through our study period (2004–2008), including livestock exclusion, fencing and planting of native plant species along inflowing stream banks and lake margins. A low-level alum dose (lake-wide concentration $0.6 \, g \, Al/m^3$) was applied in December 2003 (for details see Paul et al. 2008). During the most recent restoration attempt to control internal phosphorus loads, 110 t of Z2G1 (Blue Pacific Minerals, Matamata, New Zealand) was applied to the lake surface as a

sediment capping agent in September 2007 (Özkundakci et al. 2010).

Model description

In this study, the one-dimensional (1D) hydrodynamic model DYRESM (version 3.1.0-03) was coupled with the aquatic ecological model CAEDYM (version 3.1.0-06), both developed at the Centre for Water Research, The University of Western Australia, to simulate water quality in Lake Okaro. DYRESM resolves the vertical distribution of temperature, salinity and density in lakes and reservoirs, whereas CAEDYM simulates time-varying fluxes that regulate biogeochemical variables (e.g. nutrient species, phytoplankton biomass). The model includes comprehensive process representations for carbon (C), N, P and dissolved oxygen (DO) cycles, and several size classes of inorganic suspended solids. Several applications have been made of DYRESM-CAEDYM to different lakes (e.g. Bruce et al. 2006; Burger et al. 2007a; Trolle et al. 2008; Gal et al. 2009) and

these applications are associated with detailed descriptions of the model equations.

The biogeochemical variables in CAEDYM may be configured according to the goals of the model application and availability of data. In this study, two groups of phytoplankton were included in CAEDYM, representing generically cyanophytes (without N-fixation) and a combined group termed chlorophytes. The interactions between phytoplankton growth and losses, sediment mineralisation and decomposition of particulate organic matter influence N and P cycling in the model, as shown in the conceptual model in Fig. 2. Fluxes of dissolved inorganic and organic nutrients from the bottom sediments are dependent on temperature and NO_3-N and DO concentration of the water layer immediately above the sediment surface, with calibration of parameters specific to each application.

Model input data
In this study, the model was run at hourly time steps between July 2004 and June 2008, with daily averaged input data and daily output data at midday. Meteorological data required for the simulation period were obtained from the National Climate Data Base for the Rotorua Airport climate station *c*. 20 km north of Lake Okaro and included air temperature ($^\circ$C), shortwave radiation (W/m^2), cloud cover (fraction of whole sky), vapour pressure (hPa), wind speed (m/s) and rainfall (m). Linear interpolation between monthly samples was used to obtain daily values for stream inflow and nutrient concentrations as outlined for other model applications to Te Arawa lakes (Burger et al. 2007a; Trolle et al. 2010). Daily values for the outflow volume were calculated as a residual term of a water balance for the simulation period (methodology of Wetzel & Likens 2000), with evaporation calculated from the latent heat flux (Fischer et al. 1979) and saturation vapour pressure (Wunderlich 1972).

Model calibration and validation
DYRESM-CAEDYM was calibrated against field data for a 2-year period between July 2005 and June 2007 for variables of temperature, DO, PO_4-P, TP, NH_4-N, NO_3-N and TN at the surface (0 m) and near the bottom (14 m) of the lake, using monthly samples collected by Environment Bay of Plenty. Nutrient samples were analysed using standard analytical methods (APHA 2005). The two simulated phytoplankton groups were calibrated to represent seasonal variation of chl *a* concentrations, where cyanophytes were assumed to dominate during summer and chlorophytes during winter and early spring (Paul et al. 2008). The sum of their chlorophyll concentration was calibrated against surface chl *a* measured using an acetone extraction procedure (Arar & Collins 1997) carried out by Environment Bay of Plenty. Model parameters were adjusted manually using a trial and error approach with values within literature ranges (e.g. Schladow & Hamilton 1997; Trolle et al. 2008). The model error, represented by the root-mean-square-error (RMSE) and Pearson correlation coefficient (R) for each output variable, was quantified after each simulation for which parameter values were adjusted. Calibration continued until there was negligible improvement in RMSE and R-values. Root-mean-square-error and R-values were also compared with modelling studies in the literature to assess an acceptable model error for prediction purposes. The model was validated over two separate 1-year periods outside of the calibration period for which parameters were manipulated. The first validation period between July 2007 and June 2008 was used to evaluate the performance of the model in reproducing a period when the Z2G1 material was applied to Lake Okaro as a P-inactivation agent to reduce internal loading of P. The model was also validated with an additional period between July 2004 and June 2005, when there was an extraordinary cyanobacteria bloom consisting of an invasive, highly buoyant, N-fixing
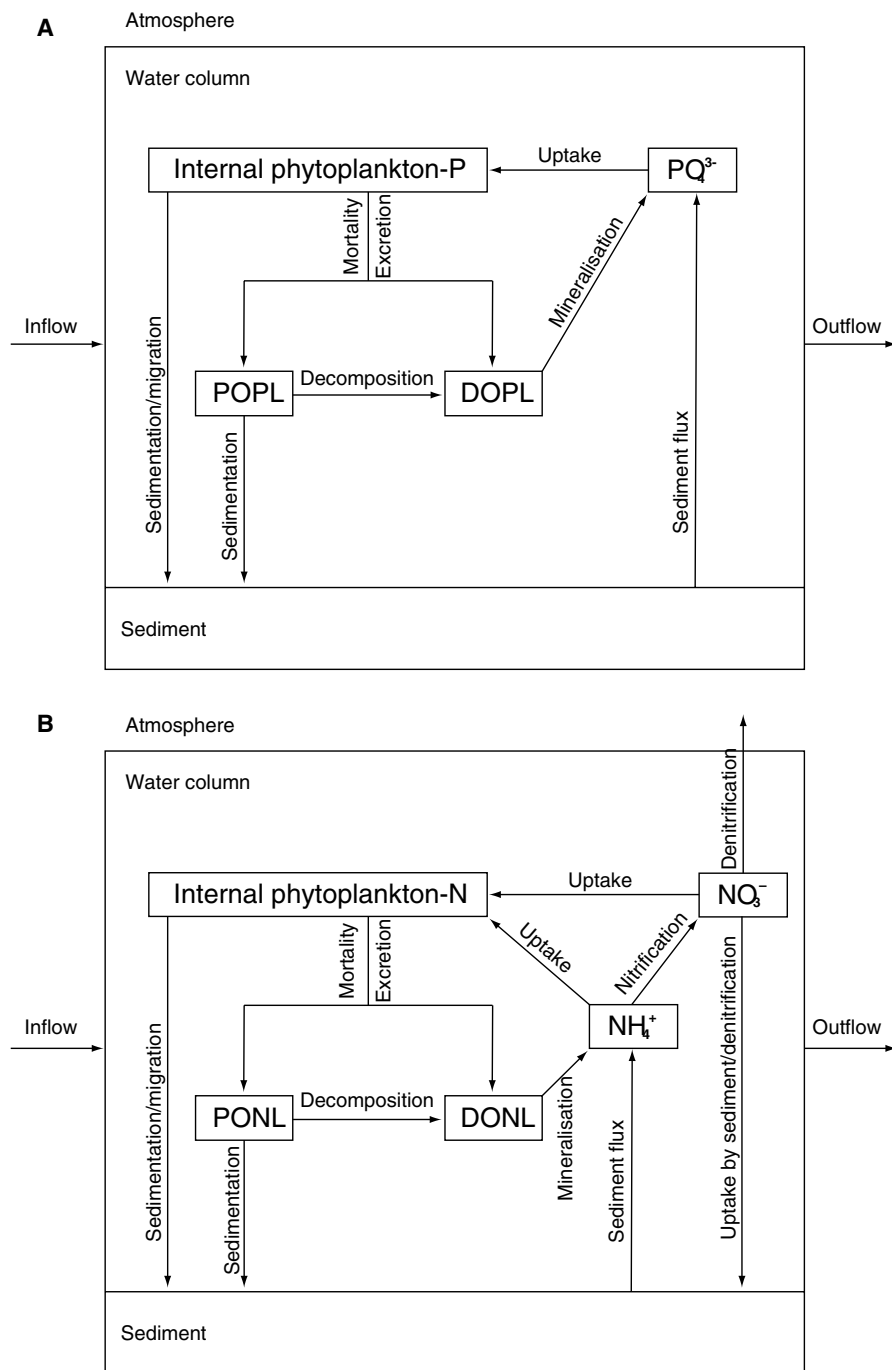
Figure 2 Conceptual models of cycles used in DYRESM-CAEDYM for the present study. **A,** Phosphorus. **B,** Nitrogen. POPL, PONL, DOPL and DONL represent particulate labile organic phosphorus and nitrogen, and dissolved labile organic phosphorus and nitrogen, respectively.

cyanobacterium, *Anabaena planktonica,* which was the dominant species in Lake Okaro over the period between November 2004 and March 2005 (Wood et al. 2005; Environment Bay of Plenty, unpublished data).

Scenarios

A series of nutrient loading scenarios were simulated by adjusting nutrient loads (internal and/or external) over the period between July 2005 and June 2008, with unadjusted loads used to represent a base scenario. Lake restoration scenarios were simulated by reducing the external and/or internal loading of either N or P (N_{ext}, N_{int}, N_{comb}, P_{ext}, P_{int} and P_{comb}), or both nutrients ($N + P_{ext}$, $N + P_{int}$ and $N + P_{comb}$), by 10%, 25%, 50%, 75% and 90% from the base simulation inputs (subscripts ext, int and comb represent external, internal and combined external/internal loading, respectively). For reduced external loading, a uniform reduction was applied to particulate and dissolved labile organic nutrients (P and N) and dissolved inorganic nutrient species (PO_4-P, NO_3-N, NH_4-N). For reduced internal loading, only dissolved inorganic nutrients were decreased by an appropriate factor applied the maximum potential sediment nutrient release rate. The TLI value was calculated for each scenario and compared with the base scenario. As Secchi depth, one of the four individual TLI indices, is not explicitly included in the model, this variable was derived from a model-predicted attenuation coefficient as:

$$Z_{SD} = \frac{\alpha}{K_d} \quad (1)$$

where z_{SD} is the Secchi depth (m), K_d is the diffuse attenuation coefficient (m^{-1}) and α is a constant (1.54 in Lake Okaro) determined by comparing field measurements of Secchi depth with corresponding values of K_d ($R =$

0.78, $p < 0.01$). In CAEDYM, K_d is calculated as:

$$K_{d(CAEDYM)} = K_W + \sum (K_a A_a) +$$
$$K_{POC}POC + K_{DOC}DOC \quad (2)$$

where K_w is the background extinction coefficient and K_a is the specific attenuation coefficient for chl a (A) for each simulated phytoplankton group (a) and K_{POC} and K_{DOC} are the specific attenuation coefficients for particulate (POC) and dissolved organic matter (DOC), respectively (Hipsey et al. 2006).

The nutrient limitation status of the two phytoplankton groups in the model was investigated by extracting daily basin-average values of the nutrient limitation functions of both N and P for each simulated phytoplankton group from the DYRESM–CAEDYM simulations. The simulated growth of phytoplankton in CAEDYM is based on a minimum expression for light, P and N:

$$\mu_{g_a} = \mu_{\max_a} \min\left[f(I)_a, f(N)_a, f(P)_a\right] f_a(T) \quad (3)$$

where $\mu_{g,a}$ is the growth rate (d^{-1}), $\mu_{max,a}$ (d^{-1}) is the maximum potential growth rate at 20°C in the absence of significant limitation by light and nutrients, f(I), f(N) and f(P) represent fractional growth limitation by light, N and P, respectively, and f(T) is a temperature function (Hipsey et al. 2006). The subscript a is used here as a generic identifier for the two simulated phytoplankton groups. A dynamic internal nutrient model in CAEDYM allows phytoplankton to have luxury nutrient stores:

$$f(j)_a = \frac{AI_{j_{MAXa}}}{AI_{j_{MAXa}} - AI_{j_{MINa}}} \left[1 - \frac{AI_{j_{MINa}}}{AI_{j_a}}\right] \quad (4)$$

where $AI_{jMAX,a}$ and $AI_{jMIN,a}$ are user-defined maximum and minimum internal nutrient concentrations, respectively, and $AI_{j,a}$ is the actual internal nutrient concentration and j represents either P or N (Hipsey et al. 2006). Growth of phytoplankton declines as internal

concentrations of the prevailing limiting nutrient (or light, Equation 3) decrease (i.e. $f(j) \to 0$), whereas growth is free of nutrient limitation when $f(j) \to 1$.

Results

Calibration and validation

The model parameters adjusted during the calibration of DYRESM and CAEDYM are presented in Table 1 and 2, respectively. The model was generally able to reproduce the magnitude and dynamics of field measurements using parameter values within the range found in the literature (e.g. Schladow & Hamilton 1997; Trolle et al. 2008). The parameter for the effect of DO on sediment ammonium release was higher than that found in other eutrophic lakes, whereas the maximum potential release rates assigned for N and P were generally lower (e.g. Burger et al. 2007a; Gal et al. 2009). The magnitude and timing of chl *a* concentrations during the calibration period were reproduced by allowing the cyanophytes luxury uptake of P (Reynolds 2006), which is reflected by a relatively high maximum internal P concentration (4.0 mg P/mg chl *a*) as observed in field studies in Lake Okaro (Lean et al. 1987). Chlorophyll *a* concentrations observed during late summer and early spring were represented in the model predominantly as contributions from the 'chlorophyte' group using parameters within

literature ranges (Schladow & Hamilton 1997; Trolle et al. 2008). The model performance of reproducing chl *a* concentration based on statistical values was comparable with other modelling studies (e.g. Burger et al. 2007a; Trolle et al. 2010).

The model simulations of temperature, DO, total nutrients and dissolved nutrients in both surface (0 m) and bottom waters (14 m) for the calibration period in Lake Okaro produced RMSE and *R*-values (Table 3) that are comparable with statistics for similar model applications (Arhonditsis & Brett 2005; Burger et al. 2007a; Trolle et al. 2010). The simulations captured the seasonal transitions of stratification, deoxygenation of bottom waters and subsequent build-up of bottom-water concentrations of PO_4-P (Fig. 3). By contrast, the timing of the increase of NH_4-N concentrations in the bottom water was not captured as accurately (Fig. 4), which was also reflected in a relatively low *R*-value of 0.83 (Table 3). The observed rapid increase in NO_3-N concentrations while DO was still present in the hypolimnion early in the stratification period was also reproduced by the model simulations (Fig. 4).

During the validation period between July 2007 and June 2008, the model simulations reproduced the field data with similar RMSE and *R*-values observed to those of the calibration period (Table 3). However, *R*-values for

Table 1 Assigned values for parameters used in DYRESM.

Parameter	Unit	Calibrated value	Reference/remarks
Critical wind speed	m/s	3.0	Spigel et al. (1986)
Emissivity of water surface	–	0.96	Imberger & Patterson (1981)
Mean albedo of water	–	0.1	Patten et al. (1975)
Potential energy mixing efficiency	–	0.2	Spigel et al. (1986)
Shear production efficiency	–	0.21	Spigel et al. (1986)
Vertical mixing coefficient	–	600	Yeates & Imberger (2003)
Wind stirring efficiency	–	0.2	Spigel et al. (1986)
Benthic boundary layer dissipation coefficient	m^2/s	7.5×10^{-6}	Calibrated
Effective surface area coefficient	m^{-2}	1.45×10^6	Calibrated

Table 2 Assigned values for parameters used in CAEDYM for Lake Okaro.

Parameter	Unit	Calibrated value	Reference source
Sediment parameters			
Sediment oxygen demand	g/m^2/day	2.0	Schladow & Hamilton (1997)
Half-saturation coefficient for sediment oxygen demand	mg/l	0.25	Schladow & Hamilton (1997)
Maximum potential PO$_4$ release rate	g/m^2/day	0.0160	
Oxygen and nitrate half-saturation for release of phosphate from bottom sediments	g/m^3	1.5	
Maximum potential NH$_4$ release rate	g/m^2/day	0.1	
Oxygen half-saturation constant for release of ammonium from bottom sediments	g/m^3	5.0	
Temperature multiplier for nutrient release	–	1.05	Robson & Hamilton (2004)
Nutrient parameters			
Decomposition rate of POPL to DOPL	day^{-1}	0.001	Schladow & Hamilton (1997)
Mineralisation rate of DOPL to PO$_4$	day^{-1}	0.025	Schladow & Hamilton (1997)
Decomposition rate of PONL to DONL	day^{-1}	0.007	Schladow & Hamilton (1997)
Mineralisation rate of DONL to NH$_4$	day^{-1}	0.01	Schladow & Hamilton (1997)
Denitrification rate coefficient	day^{-1}	0.1	
Oxygen half-saturation constant for denitrification	mg/l	2.0	
Nitrification rate coefficient	day^{-1}	0.008	
Nitrification half-saturation constant for oxygen	mg/l	2.0	
Phytoplankton parameters		Cyanophytes, chlorophytes	
Maximum potential growth rate at 20°C	day^{-1}	0.6, 1.3	Robson & Hamilton (2004)
Irradiance parameter non-photoinhibited growth	μmol/m^2/s	150, 20	Robson & Hamilton (2004)
Half saturation constant for phosphorus uptake	mg/l	0.032, 0.025	Trolle et al. (2008)
Half saturation constant for nitrogen uptake	mg/l	0.02, 0.03	Trolle et al. (2008)
Minimum internal nitrogen concentration	mg N/(mg chl *a*)	4.0, 2.0	Schladow & Hamilton (1997)
Maximum internal nitrogen concentration	mg N/(mg chl *a*)	9.0, 9.0	Schladow & Hamilton (1997)
Maximum rate of nitrogen uptake	mg N/(mg chl *a*)/day	3.0, 2.0	Schladow & Hamilton (1997)
Minimum internal phosphorus concentration	mg P/(mg chl *a*)	0.2, 0.25	Schladow & Hamilton (1997)
Maximum internal phosphorus concentration	mg P/(mg chl *a*)	4.0, 2.0	Schladow & Hamilton (1997)

Table 2 (*Continued*)

Parameter	Unit	Calibrated value	Reference source
Maximum rate of phosphorus uptake	mg P/(mg chl *a*)/day	0.5, 0.25	Schladow & Hamilton (1997)
Temperature multiplier for growth limitation	–	1.05, 1.06	Schladow & Hamilton (1997)
Standard temperature for growth	°C	19.0, 20.0	Gal et al. (2009)
Optimum temperature for growth	°C	26.0, 28.0	Gal et al. (2009)
Maximum temperature for growth	°C	34.0, 34.0	Gal et al. (2009)
Respiration rate coefficient	day^{-1}	0.055, 0.055	Schladow & Hamilton (1997)
Temperature multiplier for respiration	–	1.06, 1.06	Schladow & Hamilton (1997)
Constant settling velocity	m/day	0.0, −0.43	Burger et al. (2007a)

DOPL and DONL are dissolved organic phosphorus and nitrogen, respectively.

bottom water concentrations of TN and TP were lower than for the calibration period. The model reproduced the scale of phosphate and ammonium build-up in the bottom waters during the validation period between 2007 and 2008, despite the application of Z2G1 to Lake Okaro in September 2007. Attempts to adjust the maximum potential release rates for both PO_4-P and NH_4-N did not result in better correspondence between model output and field measurements.

The other validation period between July 2004 and June 2005 produced generally higher RMSE and lower *R*-values than for the calibration period (Table 3). In particular, the model did not reproduce a peak of chl *a*, which was dominated by the invasive, highly buoyant and N-fixing cyanobacterium, *A. planktonica*, between November 2004 and March 2005 (Environment Bay of Plenty, unpublished data). The simultaneous peaks of surface TP and TN concentrations, which were likely

Table 3 Statistical comparison between model simulations and field data of surface (0 m) and bottom (14 m) waters in Lake Okaro using root-mean-square-error (RMSE), which has the same unit as the variable estimated and Pearson correlation coefficient (*R*) for each variable.

|	Calibration (2005–2007)				Validation (2007–2008)				Validation (2004–2005)			
	Surface waters		Bottom waters		Surface waters		Bottom waters		Surface waters		Bottom waters	
	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE	*R*	RMSE	*R*
Temperature (°C)	0.822	0.99	0.786	0.99	1.165	0.98	0.723	0.90	0.801	0.99	1.176	0.98
Dissolved oxygen (mg/l)	1.814	0.39	2.205	0.83	1.781	0.72	2.952	0.82	2.242	0.34	2.665	0.85
Phosphate (mg/l)	0.014	0.83	0.064	0.93	0.018	0.44	0.064	0.85	0.015	0.82	0.091	0.95
Ammonium (mg/l)	0.114	0.92	0.509	0.83	0.048	0.97	0.509	0.96	0.208	0.89	0.626	0.84
Nitrate (mg/l)	0.030	0.83	0.016	0.96	0.014	0.96	0.016	0.93	0.059	0.56	0.060	0.43
Total phosphorus (mg/l)	0.018	0.91	0.064	0.81	0.028	0.88	0.064	0.79	0.040	0.29	0.087	0.80
Total nitrogen (mg/l)	0.382	0.28	0.465	0.78	0.277	0.50	0.465	0.67	0.851	−0.19	0.988	0.74
Chlorophyll *a* (mg/l)	13.519	0.07	–	–	23.774	0.59	–	–	90.147	−0.17	–	–
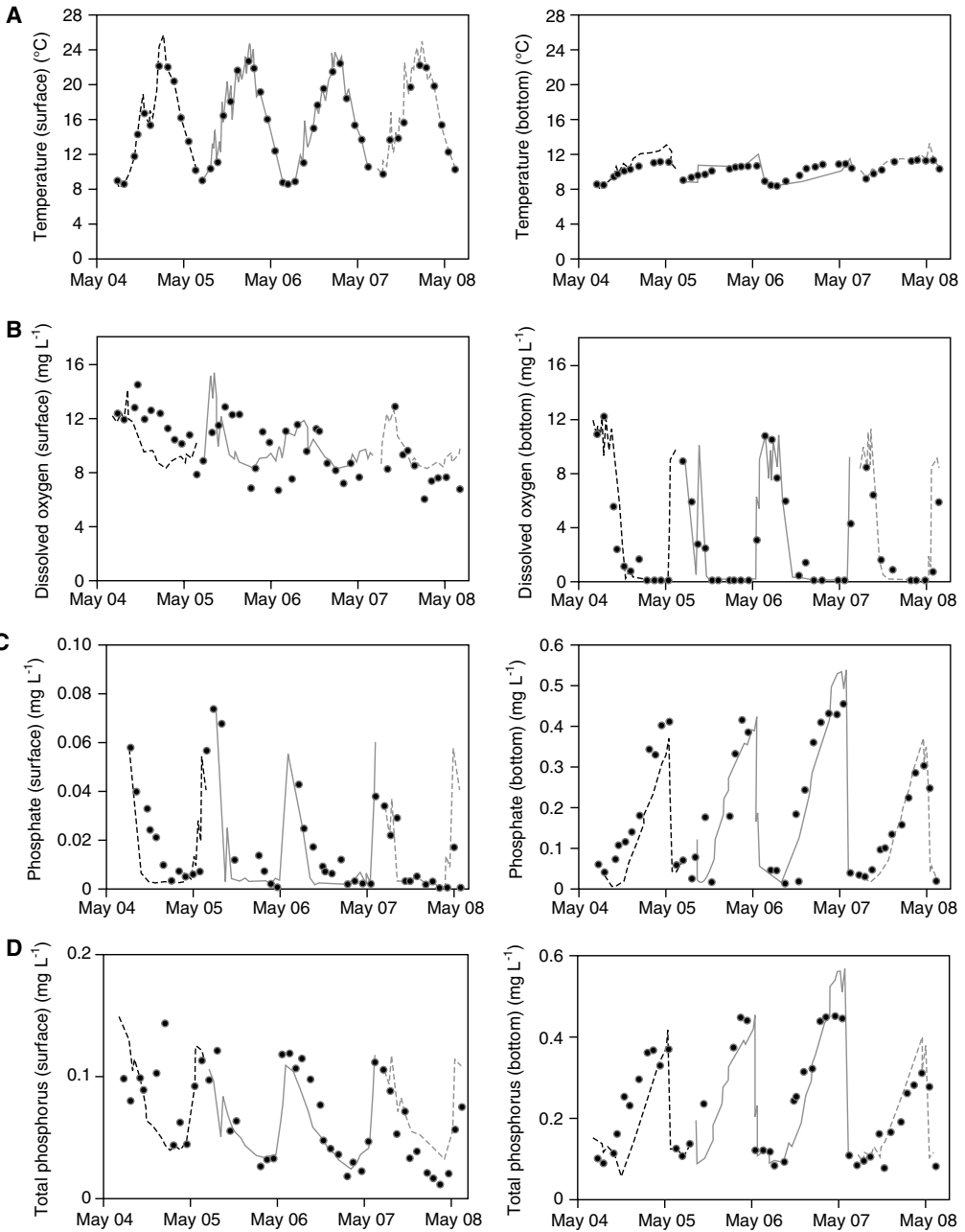
Figure 3 Comparison of model simulation results (grey lines) against field observations (black circles) in the surface (0 m) and bottom (14 m) waters of Lake Okaro during the calibration period (solid grey line) and validation periods (dashed grey and black line). **A,** Temperature. **B,** Dissolved oxygen. **C,** Phosphate. **D,** Total phosphorus.
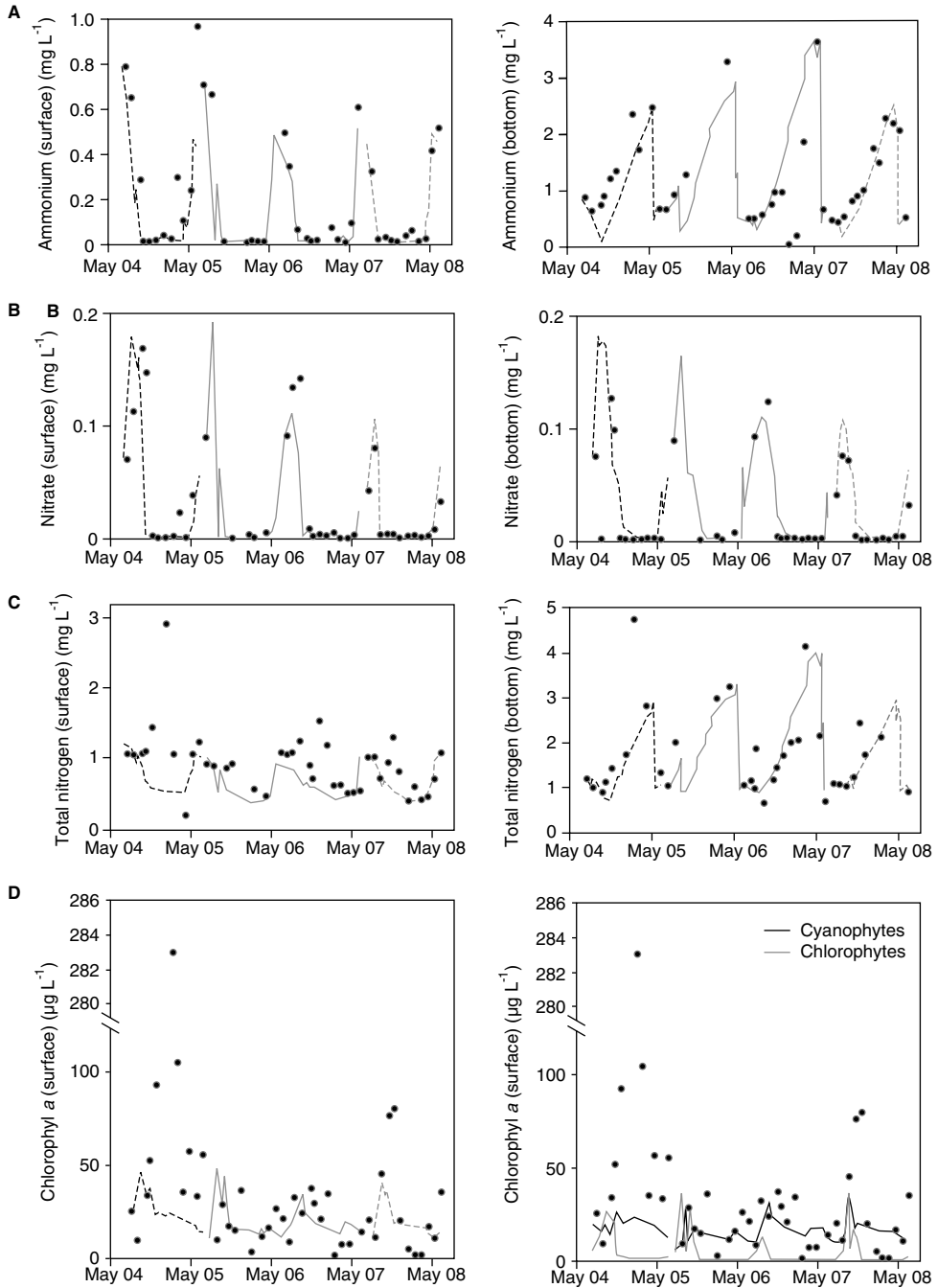
Figure 4 Comparison of model simulation results (grey lines) against field observations (black circles) in the surface and bottom waters of Lake Okaro during the calibration period (solid grey line) and validation periods (dashed grey and black line). **A,** Ammonium. **B,** Nitrate. **C,** Total nitrogen. **D,** Surface water chlorophyll *a*.

associated with the substantial phytoplankton biomass of *A. planktonica* observed during this period, were also not reproduced by the model.

Base scenario

Over the entire base scenario period (July 2005–June 2008), average TP $(63.5\,mg/m^3)$ and chl *a* concentrations $(19.3\,mg/m^3)$ were in the supertrophic range according to the TLI value for TP (Burns et al. 1997) and chl *a* $(6.0 > TL_{TP}, TL_{chla} > 5.0;$ Fig. 5). The average TN concentration was $652\,mg/m^3$, in the eutrophic range $(5.0 > TL_{TN} > 4.0)$, while Secchi depth averaged 2.6 m, which was also in the eutrophic range $(5.0 > TL_{SD} > 4.0)$. The TLI value for the base scenario averaged 4.97, slightly lower than the TLI calculated from measured data (5.08) over the same period.

Cyanophytes generally dominated chl *a* concentrations for the base scenario and comprised 80% on average of the total chl *a* concentration over the entire simulation period. The model output used to determine nutrient limitation status of the two simulated phytoplankton groups suggests that N was more often likely to limit growth of cyanophytes than P (i.e. $f(N) < f(P)$) for the majority of the simulation period (Fig. 6). Nitrogen limitation for cyanophytes increased (i.e. decreasing $f(N)$) during stratification but neither N or P was strongly limiting during mixing periods (i.e. $f(N), f(P) \rightarrow 1$). Growth of the 'chlorophyte' group was mostly limited by P over N (i.e. $f(P) < f(N)$) with limitation strongest (i.e. low $f(P)$) during stratification and least (i.e. $f(P) \rightarrow 1$) when the lake was isothermal.

Nutrient loading reduction scenarios

Model simulations show that reducing N and/or P loading produce the expected decrease in annual average water column concentrations of TN and TP, but at a lower relative rate than the corresponding percentage of reduction in external and/or internal loading (Fig. 5).

Reducing external loading would generally be less effective in reducing water column TP, TN and chl *a* concentrations relative to an equivalent reduction in internal loading. Generally, chl *a* concentrations would decrease more in response to a given percentage loading reduction of N compared with P. Not surprisingly, a combined reduction of external and internal loading for both N and P would be most effective in reducing annual average water column concentrations of TP, TN and chl *a*.

Annual average TP concentrations in Lake Okaro would generally remain in the eutrophic to supertrophic range, according to the TLI value for TP $(5.0 > TL_{TP} > 4.0$ and $6.0 > TL_{TP} > 5.0$, respectively; Burns et al. 1997), until P_{comb} is reduced by 90% (Fig. 5), when the trophic level range $(3.0 < TL_{TP} < 4.0)$ indicates that a mesotrophic state would be attained. Total N concentrations would usually be in the eutrophic range according to the TL_{TN}, but could fall into a mesotrophic category $(3.0 < TL_{TN} < 4.0)$ when N_{int}, N_{comb}, $N + P_{int}$ and $N + P_{comb}$ are reduced by more than 75% (Fig. 5). Annual average water column concentrations of chl *a* would be in the supertrophic range until N_{int}, N_{comb}, $N + P_{int}$ and $N + P_{comb}$ and P_{comb} are reduced by more than 75% and TLI values for chl *a* could fall into the eutrophic range $(5.0 > TL_{Chla} > 4.0)$. Water quality indices could be reduced most in scenarios when N and P loadings were reduced simultaneously. Generally, reduction in N loading would be more effective in increasing Secchi depth transparency than P loading reduction. TLI values would generally be in the eutrophic range for all scenarios except for $N + P_{comb}$ at 90%, when the TLI would correspond to a mesotrophic state $(3.0 < TLI < 4.0;$ Fig. 7). Reduced $N + P$ internal loading would be more effective in reducing TLI values than the equivalent fractional reduction of external $N + P$ loading alone.
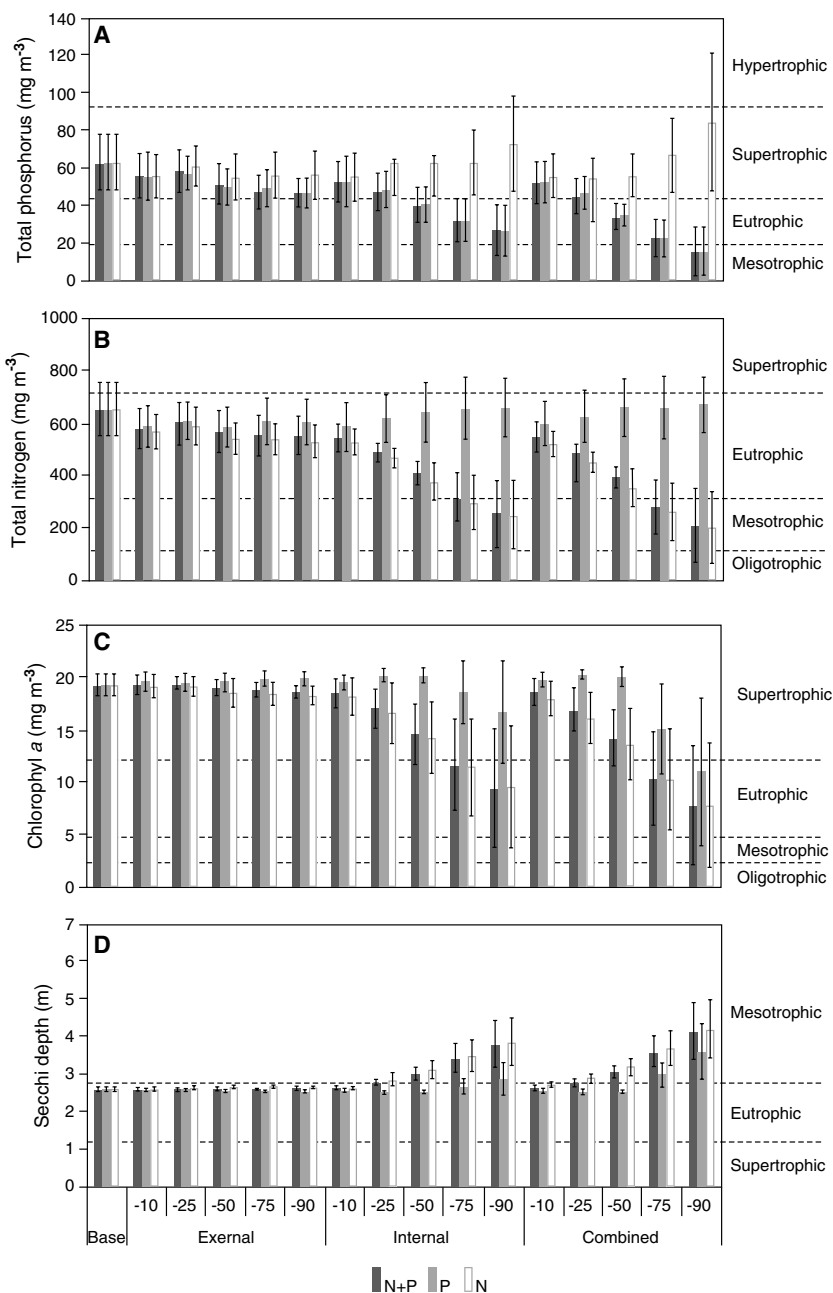
Figure 5 Simulated annual average total phosphorus, total nitrogen, and chlorophyll *a* concentrations (mg/m³) and Secchi depth (m). **A,** Total phosphorus. **B,** Total nitrogen. **B,** Chlorophyll *a*. **D,** Secchi depth. Inter-annual variation is represented by ± one standard deviation compared with the base scenario (July 2005–June 2008) for simultaneous reduction of both nitrogen (N) and phosphorus (P) and individual reduction of P or N for reductions in external loading, internal loading, and a combined reduction of both external and internal loading (−10%, −25%, −50%, −75% and −90%).
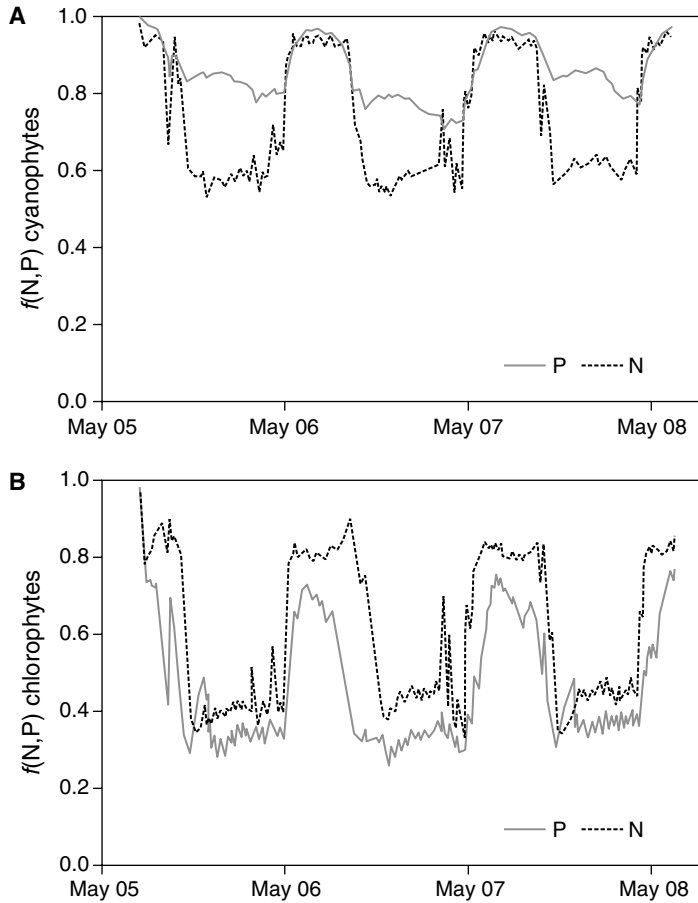
Figure 6 Limitation function (*f*) of phosphorus (P) and nitrogen (N) for the base scenario of July 2005–June 2008. **A,** Cyanophytes. **B,** Chlorophytes.

Effect of nutrient load reductions on nutrient limitation

The proportion of nutrient limitation over the simulation period for cyanophytes would change from almost entirely N-limited to almost entirely P-limited in scenarios when P_{int} and P_{comb} exceeded a 75% reduction. Nitrogen limitation of cyanophytes would predominate in all scenarios when only N or N + P was reduced. A change in nutrient limitation from almost exclusively P-limited to almost entirely N-limited would be observed for chlorophytes in scenarios when external and/or internal N loading was reduced by more than 50%. Chlorophytes were predominantly P-limited

for all other scenarios. The proportion of the total chl *a* concentration represented by cyanophytes (80% in the base scenario) would decrease with greater N load reductions (as low as 70%) whereas the proportion of cyanophytes would increase with increasing P loading reduction (as high as 87%).

Discussion

In this study, DYRESM-CAEDYM was applied to Lake Okaro to investigate the need for nutrient load reduction to improve the trophic state in the lake, which was represented by the TLI. In other studies, it has been suggested that
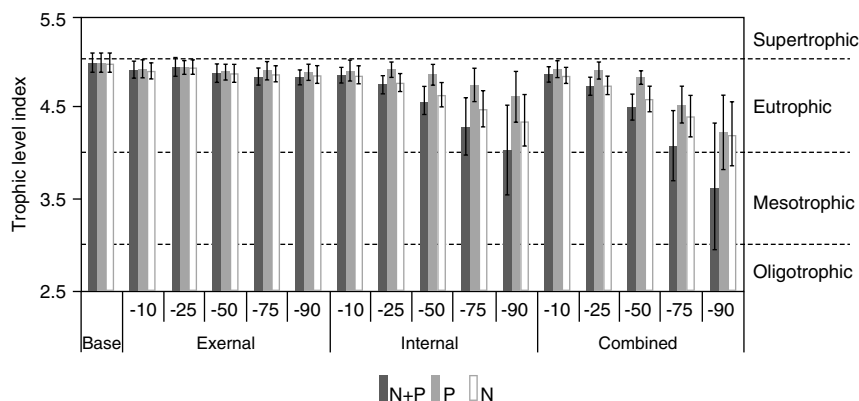
Figure 7 Simulated Trophic Level Index values. Inter-annual variation is represented by ± one standard deviation compared with the base scenario (July 2005–June 2008) for simultaneous reduction of both nitrogen (N) and phosphorus (P) and individual reduction of P or N for reductions in external loading, internal loading, and combined reduction of both external and internal loading (−10%, −25%, −50%, −75% and −90%).

a simultaneous reduction of both N and P loads would be more successful in reducing phytoplankton than the reduction of one of these nutrients alone (Lewis & Wurtsbaugh 2008). This strategy appears to be suitable for Lake Okaro, where a combined N + P loading reduction simulation resulted in a greater decrease of TLI values than the equivalent reduction of either N or P loading. This study also shows that P loading reductions have to be substantial to induce dominance of P-limitation to compensate for high background levels of P that saturate demand.

Model performance and constraints

While the model generally reproduced the timing and magnitude of the simulated variables, there were some discrepancies between the model output and field measurements. There were occasionally higher surface concentrations of phosphate in the winter mixed period in the model simulation compared with field data, mostly during the calibration period. This could be partially an effect of the relatively simplistic process representation of sediment nutrient dynamics in CAEDYM. The model regulates the sediment phosphate release according to

concentrations of DO and nitrate, and temperature in the overlying water layer. Changes in sediment P release in the model thus reflect only the relevant water layer variables and not any changes in sediment P content (e.g. Hupfer & Lewandowski 2008) or related processes, such as the time scales on which P is resupplied from sediments at depths of up to 20 cm (Søndergaard et al. 2003). A further confounding factor is that the simulation falls within a period when several different restoration procedures were implemented in Lake Okaro, commencing in 2003 (Environment Bay of Plenty 2006). Changes in external nutrient loading will likely feed back to sediment nutrient releases, leading towards a new equilibrium between external and internal loading (Søndergaard et al. 2003). As there is no such feedback on the bottom sediment composition in the current version of CAEDYM, the scenarios with combined nutrient reduction (i.e. external and internal loading) may perhaps best reflect this feedback, however, without demonstrating the typical period of 10–15 years that could be expected before small to medium-sized lakes reach a new equilibrium state in response to reduced loading (Jeppesen et al. 2005). The inclusion of a dynamic response of sediment

nutrient releases in the model to changes in sedimentation in the water column after reduced external loading as well as sediment diagenetic processes could, however, provide a better understanding of the temporal variability of sediment nutrient releases.

Conceptual simplifications of the system being modelled are unavoidable (Harris 1994) and it is important to acknowledge the effect of these simplifications on the outcome of various model scenarios. Data for fish, submerged macrophytes and zooplankton were not available for the simulation period, and were not included in the conceptual model. The impact of major nutrient loading changes on phytoplankton community structure can be substantial (Schindler 2006) and food webs can undergo significant shifts in their trophic cascade by, for example, increased zooplankton grazing pressure on smaller phytoplankton following nutrient load reductions (Carpenter 2003; Jeppesen et al. 2005) that may not be represented adequately with a dynamic ecosystem model such as DYRESM-CAEDYM (Trolle et al. 2008). Therefore, the phytoplankton response to reduced nutrient loading may be underestimated in the model, as no higher trophic levels and sediment diagenetic processes were included in the conceptual model.

A further limitation of most ecosystem models is their inability to predict ecosystem changes that may occur because of the introduction of a new species. For example, DYRESM-CAEDYM did not reproduce to any great extent the chl *a* peak observed in December 2004. During this period there was a dense (>70,000 cells/ml) bloom of *A. planktonica* in the lake. This species was first detected in New Zealand and in Lake Okaro in 2000, and has since spread rapidly throughout the North Island of New Zealand (Wood et al. 2005; Environment Bay of Plenty, unpublished data). It has been reported to dominate the phytoplankton community for short periods within 2–3 years of its introduction into a water body (Ryan et al. 2003; Wood et al. 2010), after which time its dominance tended to decline,

supposedly because of a natural response and adaptation of the overall lake ecosystem to a new invasive species. Although *A. planktonica* still occurs in Lake Okaro, blooms of the magnitude reported in December 2004 have not recurred to date (Environment Bay of Plenty, unpublished data).

The inclusion of an additional phytoplankton group in the conceptual model could not be justified based on the lack of differentiation of total chl *a* concentrations to taxonomic level. However, different phytoplankton groups or even different species within groups (e.g. *Microcystis* vs *Anabaena* amongst the cyanobacteria) may have different nutrient requirements (Reynolds 2006). As *A. planktonica* is heterocystous and can potentially supplement nitrogen requirements through N-fixation when inorganic nitrogen concentrations are low (Wood et al. 2010), the model in its present form, with cyanophytes not assigned an N-fixation function, may require further adaptive refinement. This limitation may have had subsidiary effects, for example, compromising the ability to reproduce accurately N concentrations in the water column because N-fixation may account for considerable proportions (6–82%) of total N loads to a lake (Oliver & Ganf 2000).

The question of whether dynamic, process-based ecosystem models have the desired predictive power to forecast the future (e.g. restoration scenarios) has been discussed previously (Flynn 2005; Jakeman et al. 2006). Validating a calibrated model against an independent data set to determine if the model not only fits measured data but also functions adequately (e.g. with respect to trophic structure) is often thought to be a satisfactory performance evaluation (Arhonditsis and Brett 2004; Robson et al. 2008). However, even validation cases are only applicable to those conditions under which the model is tested and consistent with the modelling objectives (Power 1993; Rykiel 1996). Based on the statistical evaluation of the model performance in this study, the model uncertainty may remain

relatively high and comparison of model performance between studies could be ambiguous because of differences in conceptual complexity and model formulation. However, the operational validity of the model could be considered adequate, considering that model parameters were kept within the values found in the literature. We thus reason that the model accuracy was sufficient to meet our objectives of contributing information on long-term management strategies as opposed to an ability to predict the exact timing and magnitude of individual algal bloom events. The predictions presented in this study should still be viewed with some caution, however, particularly in light of the influence of a new phytoplankton species, which initially out-compete endemic species.

The implications of model scenarios for lake restoration

The model simulations indicate that water column TN, TP and chl *a* concentrations change little with a reduction in external loading compared with internal loading. A modelling study of eutrophic Lake Rotorua by Burger et al. (2007a) also found that reducing external loading had only a minor impact on chl *a* concentrations compared with the same percentage reduction in internal loading. Direct comparisons between percentage reduction of external and internal nutrient loading can, however, be somewhat misleading. External nutrient loading includes various fractions of dissolved and particulate organic and inorganic nutrients, which may not be immediately available for phytoplankton and may be lost from the system because of settling of particulate organic matter. By contrast, internal loading in this model comprises entirely of dissolved inorganic nutrient species.

The control of external N loading may in some circumstances be more easily achieved than control of P loading. Constructed wetlands, for example, are generally effective in reducing N loading via denitrification, whereas

P retention can be relatively short-lived and the saturation of the soil substrate of the wetland can potentially lead to an increase in P loading (Fink & Mitch 2004). The management of nutrient loads is also a sensitive issue because of the national importance of pastoral farming to the New Zealand economy. For the Te Arawa lakes in the Volcanic Plateau, which is an area that contains P-rich volcanic ash in the soil profile, a considerable portion of N inputs to the lakes originate from diffuse sources and relate to increases in N fertiliser additions driven by ongoing intensification of agriculture (White et al. 1985; Hamilton 2005; Parliamentary Commissioner for the Environment 2004). The reduction of external nutrient loading, however, has to be a priority in the long term, since the persistent supply and decomposition of nutrient rich organic material to the sediment may limit the longevity of effective restoration methods addressing internal loading.

An increase in N-limitation as a result of N loading reduction could promote dominance of N-fixing cyanobacteria (Smith 1983; Howarth et al. 1988; Schindler et al. 2008) resulting in cyanobacterial blooms, especially when there are high levels of inorganic P (e.g. in Lake Okaro). Schindler et al. (2008), for example, indicated with a 37-year experiment of managing nutrient inputs to a single lake, that the control of N loading alone could promote eutrophication. It appears to be counter-intuitive to reduce N loading alone, considering the risk of promoting N-fixing cyanobacteria in an ecosystem which is already eutrophic. However, while reducing P loading alone has been shown to result in major reductions in chl *a* concentrations in a series of Danish lakes (Jeppesen et al. 2007), it may be difficult to achieve P-limitation in many lakes of the central North Island of New Zealand, which have a tendency to be N-limited or co-limited by both N and P because of P-rich volcanic soils (White et al. 1985; Burger et al. 2007b; Abell et al. 2010). This trend towards N-limitation may be exacerbated by the dominance of cyanobacteria with the ability for luxury P

uptake (Reynolds 2006). On the basis of our model results, the control of both N and P appears to be more effective in reducing phytoplankton biomass more than N or P alone, tending to affirm a N + P control paradigm (Lewis & Wurtsbaugh 2008).

While the phytoplankton nutrient limitation functions in DYRESM-CAEDYM (Equation 4) are essential for understanding the seasonal dynamics of the modelled phytoplankton community, they are typically not presented in modelling studies (e.g. Burger et al. 2007a; Trolle et al. 2008, Trolle et al. 2010; Gal et al. 2009). Ideally, one would be able to validate individual processes sequentially, but for many of the processes included in DYRESM-CAE-DYM (e.g. mineralisation and settling of organic matter, sediment nutrient releases, phytoplankton growth etc.), no data were available to validate these fluxes or nutrient limitation function explicitly. Instead, we calibrated model parameters (i.e. $AI_{jMAX,a}$ and $AI_{jMIN,a}$) within given ranges defined by previous field and laboratory studies and applied in other modelling studies. As a consequence, evaluation of the nutrient limitation functions is partially theoretical and should be addressed with some caution. We believe that our work now throws out a challenge for other studies to validate the nutrient uptake model with observed bioassay data.

Conclusions

The model application to Lake Okaro suggests through a series of nutrient loading reduction scenarios that the lake will remain eutrophic until external and internal nutrient loadings of both N and P are reduced by more than 75%. According to the model, N loading reduction may be more successful in improving water quality measured by the TLI than reducing P loading alone. Evaluation of the nutrient limitation status of the simulated phytoplankton groups revealed that N is a major limiting factor for cyanobacteria growth while P limitation of this dominant phytoplankton

group would require severe reductions in P loadings.

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