Benthic nutrient fluxes in a eutrophic, polymictic lake

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Abstract Sediment release rates of soluble
reactive phosphorus (SRP) and ammonium
(NH_4) were determined seasonally at three sites
(water depth 7, 14 and 20 m) in Lake Rotorua
using in situ benthic chamber incubations.
Rates of release of SRP ranged from 2.2 to
85.6 mg P m^{-2} d^{-1} and were largely independent
of dissolved oxygen (DO) concentration. Two
phases of NH_4 release were observed in the
chamber incubations; high initial rates of up to
2,200 mg N m^{-2} d^{-1} in the first 12 h of deploy-
ment followed by lower rates of up to
270 mg N m^{-2} d^{-1} in the remaining 36 h of
deployment. Releases of SRP and NH_4 were
highest in summer and at the deepest of the three
sites. High organic matter supply rates to the
sediments may be important for sustaining high
rates of sediment nutrient release. A nutrient
budget of Lake Rotorua indicates that internal
nutrient sources derived from benthic fluxes are
more important than external nutrient sources to
the lake.

Keywords Nitrogen · Phosphorus · Sediment ·
Benthic chambers · Internal load ·
External load · Lake Rotorua

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Introduction

Sediment fluxes of nitrogen (N) and phosphorus
(P) to the overlying water column may support a
significant fraction of the total nutrient require-
ments for primary productivity in lotic systems
(Marsden, 1989; Søndergaard et al., 1999). Pro-
longed external loading may ultimately produce
elevated levels of nutrients in bottom sediments
that, under certain environmental conditions such
as anoxia, are remobilised and returned to the
water column (Boström et al., 1988). Thus sus-
tained high concentrations of water column nutri-
ents have been observed in many lakes despite
large reductions in external loads, particularly
from point source inputs (Marsden, 1989; Sønderg-
aard et al., 2003). Studies of lake nutrient cycling,
particularly in the Northern Hemisphere, empha-
sise P release because of its impact on phytoplank-
ton production (e.g., Kleeberg & Kozerski, 1997;
Søndergaard et al., 2003). However, N can also

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

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

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

the sediments and overlying water (see review by Tengberg et al., 1995), while incorporating a large sediment surface area as well as the natural light and temperature conditions of the lake.

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

Study site

Lake Rotorua is a large (79.8 km^2), shallow (mean depth 10.5 m), polymictic lake in central North Island, New Zealand (Fig. 1). It is eutrophic (Rutherford et al., 1996) and annual mean water column concentrations of total phosphorus (TP) and total nitrogen (TN) are 0.055 mg L^{-1} and 0.814 mg L^{-1}, respectively (Burger et al., 2005). The Lake Rotorua catchment area of 425 km^2 is dominated by agriculture (48%) and plantation forestry (23%). There are nine major inflows to the lake (mean discharge 0.22–2.75 m^3 s^{-1}) as well as 17 minor inflows, including urban drains and geothermal springs (mean discharge <0.06 m^3 s^{-1}). Until 1991 Lake Rotorua received discharges of wastewater from Rotorua city (population 60,000), which contributed annual nutrient loads of 35 tonnes TP yr^{-1} and 150 tonnes TN yr^{-1} (White et al., 1992). While removal of wastewater discharges was expected to improve lake water quality (Rutherford et al., 1996), nutrient concentrations have remained high and there are frequent summer blooms of cyanobacteria (Burger, 2006).

Methods

Sediment nutrient fluxes

Benthic chambers were deployed at three sites (Fig. 1) on four occasions between February 2003

Fig. 1 Map of Lake Rotorua showing chamber deployment sites: Site 1 (depth 7 m), Site 2 (depth 14 m) and Site 3 (depth 20 m). The 20 m depth contour is also shown
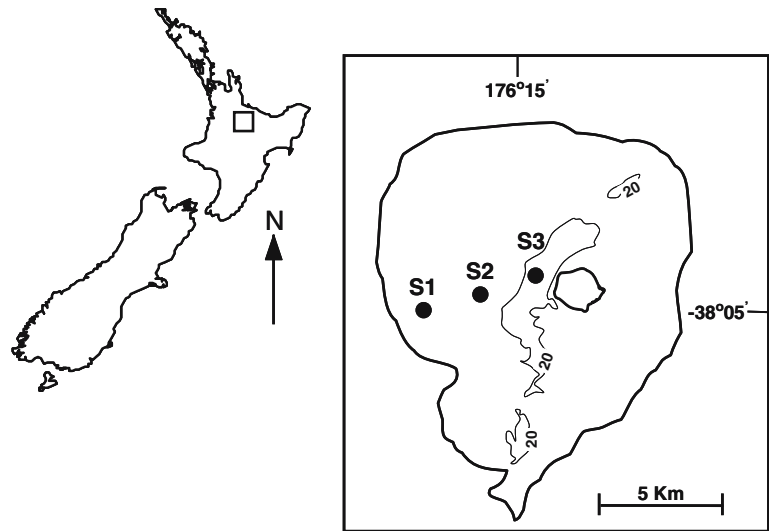
and January 2004 (Table 1). Sites were chosen to reflect the natural variability in mixing regime, from permanently well mixed and oxygenated in shallow regions (site 1: depth 7 m), to periodically stratified and anoxic in deeper regions (site 2: depth 14 m and site 3: depth 20 m). At sites 1 and 2 both light chambers (circular, 6 mm acrylic plastic, encompassing sediment area 0.111 m^2 and water volume 17.76 L) and dark chambers (circular, 8 mm PVC, encompassing sediment area 0.116 m^2 and water volume 18.53 L) were deployed in duplicate. At site 3 (depth 20 m), where light at the sediment surface was <1% of photo-

synthetically available radiation (PAR) at the water surface (Table 1), only light chambers were deployed. Two chambers were deployed at site 3 in all periods except February 2004, when four chambers were used.

On each sampling date chambers were deployed between 08:30 and 14:00 h, depending on weather conditions. Deployment was assisted by SCUBA divers to minimise sediment disturbance during insertion of the chambers into the sediments. Chambers were pushed into the sediments to a depth of 80 mm, corresponding to the position of a flange on the outside of each

Table 1 Mean concentrations of ammonium (NH_4), soluble reactive phosphorus (SRP), nitrate (NO_3) and dissolved oxygen (DO) in bottom waters at sites 1, 2 and 3 at the start of each incubation

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

Temperature (T) and photosyntheticaly available radiation (PAR) are mean values in bottom waters derived from daily CTD casts during each chamber deployment

chamber. After chamber insertion, taps (Ø = 9 mm) in the chamber lids were left open for 20 min before the start of each experiment. Water in the chambers was mixed throughout the experiment with a submersible 6 V DC pump (LVM Ltd), which circulated water for 5 s each minute. Laboratory trials showed that this flow regime maintained well-mixed conditions inside the chambers without inducing sediment resuspension. Bottom water samples were also collected during all deployments, and incubated in duplicate dark and light 1 L PET® bottles alongside the chambers, to measure water column nutrient regeneration rates in the absence of bottom sediments.

Chambers were sampled four times daily, depending on incubation start time and weather conditions; usually at 07:00, 11:00, 15:00 and 19:00 h, over 2 days. This deployment period was sufficient to create anoxic conditions in the chambers at sites 2 and 3 during summer incubations, thereby simulating release rates normally observed during natural stratification events when bottom waters become anoxic (Burger et al., 2005). Water was transported from the chambers to the surface under reduced pressure through clear plastic tubing (Ø = 4 mm) and collected in an in-line trap after flushing each line. A small external opening (Ø = 4 mm) in the chamber lid allowed replenishment of water sampled from the chamber with water from the depth of deployment. A sample volume of up to 60 ml was collected from each chamber on each sampling occasion, of which 25 ml was immediately separated for analysis of dissolved oxygen (DO) concentration (YSI Instruments, Model 50, probe electrode model 5739). The remaining sample was filtered through GF/C 25 mm diameter syringe filters and placed on ice before return to the laboratory, where filtrate was frozen before analysis for NH_4, NO_3 and SRP on a Lachat Instruments flow injection analyser (FIA, Zellweger Analytics, 2000). On three sampling occasions (August and November 2003, and January 2004), in situ DO sensors (Van Essen Instruments) were also used to record changes in DO concentration at 15 min intervals in a light and a dark chamber (sites 1 and 2) or in all chambers (site 3).

Sediment NH_4 and SRP fluxes were calculated from the slope of linear regressions of chamber nutrient concentrations with time (Gibbs et al., 2002). After correcting for the effect of dilution associated with sample removal, rates of change of nutrient concentrations in the chamber were divided by the sediment surface area in the chambers, to give an aerial release rate. Changes in nutrient concentrations in control bottles incubated alongside the chambers during each deployment were <0.020 and <0.006 mg L^{-1} d^{-1} for NH_4 and SRP, respectively, and were subtracted from the final sediment release rate. Fluxes of NO_3 not calculated as concentrations in the chambers were less than 5% of those of NH_4 and were often below analytical detection limits (0.001 mg L^{-1}). Where in situ DO sensors were deployed inside the chambers, sediment oxygen demand (SOD) was calculated from the slope of linear regressions of chamber DO concentrations over the time period 0.25–2.25 h. For remaining deployments, SOD was calculated from the rate of change of DO between the first and second measurements (i.e., c. 4 h). Differences in SRP and NH_4 release rates and SOD between sites, period, and sites × period were examined using a two-way analysis of variance (ANOVA) with post-hoc analysis using the Tukey HSD test with a confidence interval of 95%. Prior to ANOVA analyses, data were examined for normality and homogeneity of variance by visual inspection of residuals and no transformations were necessary.

Chamber water displacement

Rates of water dilution in each chamber were assessed on one sampling occasion (February 2003) by injecting the chambers with a bromine tracer (LiBr at 5 µg L^{-1}) at the start of each deployment, and measuring changes in Br concentration at 0.5 and 48 h. Concentrations of Br were analysed by mass spectroscopy and varied little (<0.003 µg Br L^{-1}) from the dilution rate calculated using the total volume of water displaced from each chamber during sampling. Groundwater flows were also assessed using observations by divers of water bladders placed on the chamber outlet for

20 min at 48 h during the same deployment. The bladders did not inflate, indicating that groundwater influxes were likely to be low.

Water column measurements

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

Results

Water column variables

Water column profiles of temperature and DO concentration, collected from each site at the

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

Bottom water concentrations of NH_4, SRP and NO_3, corresponding to initiation of each chamber deployment, varied between seasons and sites (Table 1). Mean concentrations of SRP over all seasons were highest at site 3 (0.042 mg L^{-1}) followed by site 2 and site 1 (0.022 and 0.018 mg L^{-1}, respectively). Nutrient concentrations in bottom waters were lowest in August
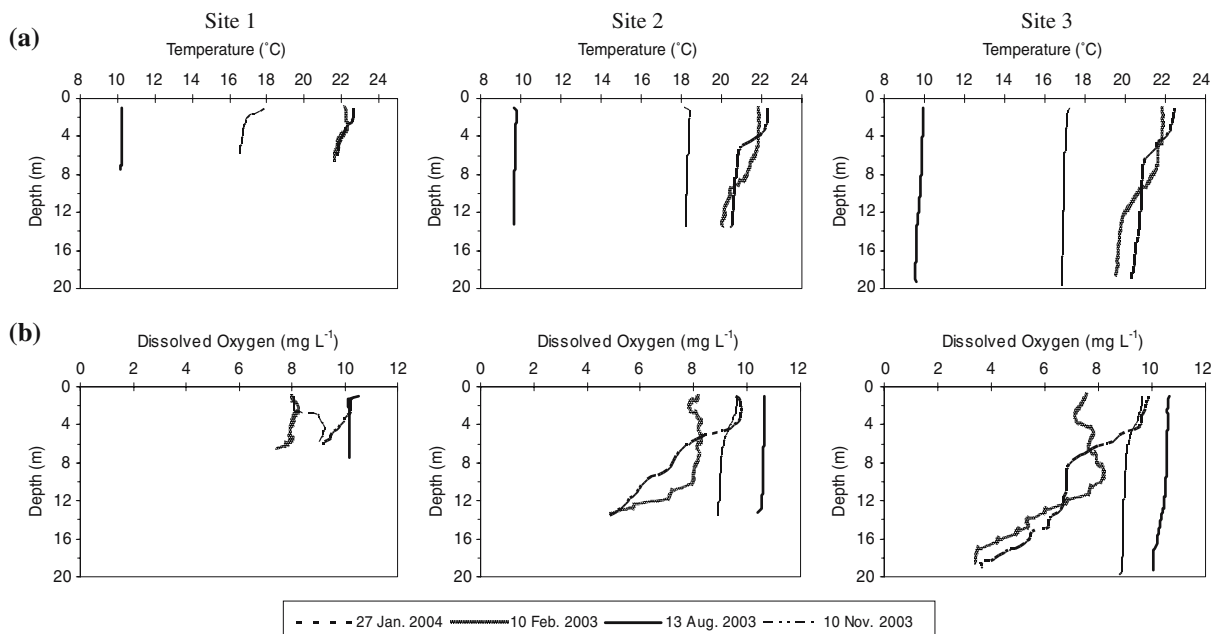

Fig. 2 Water column profiles of (a) temperature and (b) dissolved oxygen concentration at sites 1, 2 and 3 on 10 February, 13 August and 10 November 2003, and 27 January 2004

2003 (winter) and highest in February 2003, when DO concentrations were low. Mean concentrations of NH_4 were also highest at site 3 (0.184 mg L^{-1}), followed by site 2 (0.171 mg L^{-1}) and site 1 (0.053 mg L^{-1}). Mean concentrations of NO_3 over the four periods were highest at site 1 (0.012 mg L^{-1}) and lowest at site 2 (0.008 mg L^{-1}). Over all periods, mean values of PAR at the depth of the chamber incubations at each site were highest at site 1 (mean 5.12 μmol quanta m^{-2} s^{-1}) followed by site 2 (0.19 μmol quanta m^{-2} s^{-1}) and site 3 (0.10 μmol quanta m^{-2} s^{-1}, Table 1).

Sediment oxygen demand

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

SRP benthic fluxes

Concentrations of SRP in the light chambers increased in a relatively linear manner over time (Fig. 3) and the rate of release did not show an obvious dependence on DO concentrations inside the chambers. Linear regressions between SRP concentrations versus time for all sites and periods yielded a mean R^2 of 0.93 (range 0.82–0.99). Sediment SRP release rates ranged between 2.1 and 85.6 mg m^{-2} d^{-1} (Table 2, Fig. 4).

Statistical analyses showed a highly significant effect of site ($P < 0.01$), period ($P < 0.01$) and site × period ($P < 0.01$) for sediment SRP releases (Table 3). Post-hoc analyses revealed release rates at site 3 (mean 44.3 mg m^{-2} d^{-1}) were significantly higher than release rates at site 2

Table 2 Mean sediment release rates for ammonium from 0 to 12 h (NH_4 1) and 12–48 h (NH_4 2), and soluble reactive phosphorus (SRP, 0–48 h) obtained with light and dark benthic chambers on four occasions between February 2003 and January 2004 as sediment oxygen uptake rate (SOD)

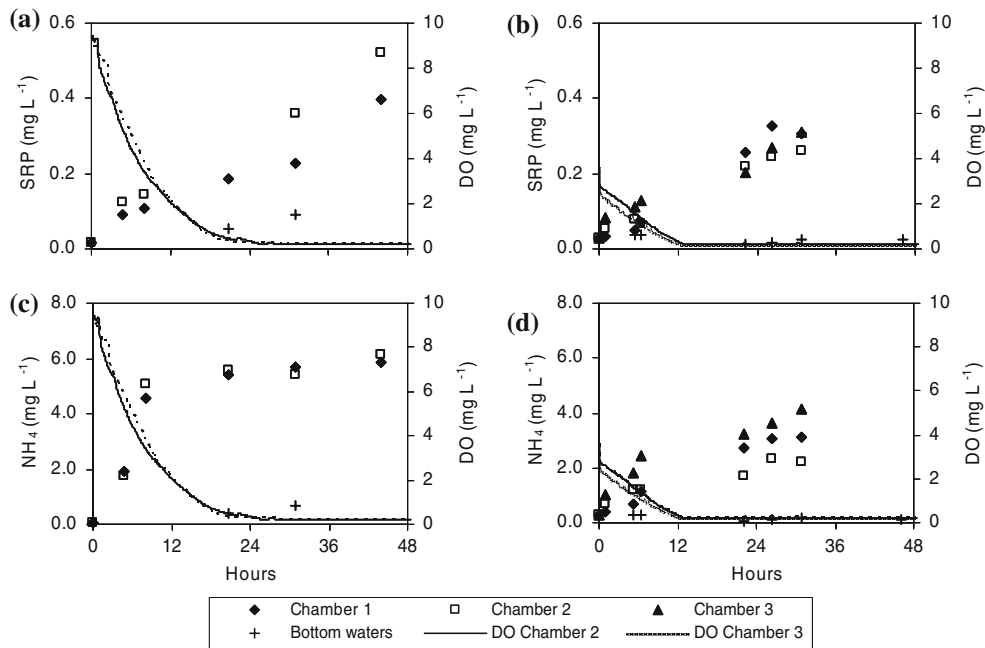| Site	Period	n	Light chambers				Dark chambers			
			NH_4 1 (mg m^{-2} d^{-1})	NH_4 2 (mg m^{-2} d^{-1})	SRP (mg m^{-2} d^{-1})	SOD (g m^{-2} d^{-1})	NH_4 1 (mg m^{-2} d^{-1})	NH_4 2 (mg m^{-2} d^{-1})	SRP (mg m^{-2} d^{-1})	SOD (g m^{-2} d^{-1})
1	10 Feb. 2003	2	414.6	70.3	10.2	0.75	415.5	109.2	6.5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

dark chambers were not used at site 3

Fig. 3 Changes in concentrations of phosphorus (SRP) and ammonium (NH$_4$), and dissolved oxygen (DO) in replicate benthic chambers and bottom waters at site 3 in November 2003 (**a**, **c**) and January 2004 (**b**, **d**)

(mean 9.3 mg m^{-2} d^{-1}) and site 1 (mean 7.7 mg m^{-2} d^{-1}) for all periods except August 2003 (Tables 2 and 3, Fig. 4). Release rates at site 3 were also significantly different between periods ($P < 0.01$), and were highest in February 2003 and lowest in August 2003. The observed rate in August 2003 was nearly 10 times lower than in all other periods (Table 2). At sites 1 and 2, SRP release rates were highest in January 2004 and lowest in August 2003 but were not significantly different between periods ($P > 0.05$).

Differences in SRP release rates between light and dark chambers were <3.7 mg m^{-2} d^{-1} at site 1 (Table 2, Fig. 5), which was not statistically significant (Table 4). In February 2003, SRP release rates at site 2 were three times higher in dark chambers (29.4 mg m^{-2} d^{-1}) than in light chambers (9 mg m^{-2} d^{-1}, Fig. 5).

NH$_4$ benthic fluxes

NH$_4$ fluxes were characterised by two rates of release (Fig. 3). The first phase from 0 to 12 h of deployment had very high NH$_4$ release, with maximum values in the light chambers of 415, 578
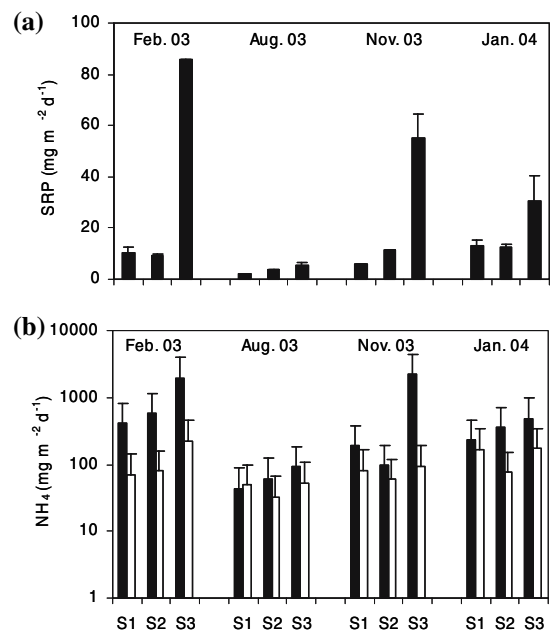

Fig. 4 Fluxes of (**a**) soluble reactive phosphorus (SRP) and (**b**) ammonium (NH$_4$), for sites 1 (S1), 2 (S2) and 3 (S3) from four periods of light chamber deployment. Error bars represent standard errors ($n = 2$–4). For NH$_4$, dark bars represent release initial release rates (0–12 h) and light bars represent secondary release rates (12–48 h)

Table 3 Two way analyses of variance between site, period and site × period for fluxes of soluble reactive phosphorus (SRP), ammonium in the phase 0–12 h (NH$_4$ 1) and subsequent phase 12–48 h (NH$_4$ 2)

Fluxes	Factor	df	MS	F	P
SRP	Site	2	1,554	58.07	<0.01
	Period	3	656	24.51	<0.01
	Site × Period	6	336	12.58	<0.01
	Error	13	27		
NH$_4$ 1	Site	2	27,97,711	201.37	<0.01
	Period	3	887,278	63.86	<0.01
	Site × Period	6	740,314	53.29	<0.01
	Error	13	13,893		
NH$_4$ 2	Site	2	11,650	5.09	0.023
	Period	3	11,625	5.08	0.015
	Site × Period	6	3,554	1.55	0.238
	Error	13	2,291		

df is degrees of freedom, MS is mean squares, F is the test statistic and P is probability

and 2,213 mg m^{-2} d^{-1} at sites 1, 2 and 3, respectively (Fig. 3). In the second phase NH$_4$ release was substantially lower, with a maximum value across all sites of 224 mg m^{-2} d^{-1} (Fig. 3).

For initial rates of NH$_4$ release, there was a significant effect of site ($P < 0.01$), period ($P < 0.01$) and site × period ($P < 0.01$) (Table 3). Initial NH$_4$ fluxes at site 3 (mean 1,187 mg m^{-2} d^{-1}) were significantly higher ($P < 0.05$) than at site 2 (mean 272 mg m^{-2} d^{-1}) and site 1 (mean 220 mg m^{-2} d^{-1}) (Tables 2 and 3, Fig. 4). Release rates between sites 1 and 2 were not significantly different. At all sites, release rates were signifi-

cantly lower in August 2003 than in all other periods. Release rates at sites 1 and 2 were highest in February 2003 and at site 3 in November 2003. The secondary release rate of NH$_4$ was also highest at site 3 in all four deployments (mean 136 mg m^{-2} d^{-1}), followed by site 1 (mean 92 mg m^{-2} d^{-1}) and site 2 (mean 62 mg m^{-2} d^{-1}, Table 2, Fig. 5). Factorial analysis of variance ($P < 0.05$) showed an effect of site and of period, but not site × period (Table 3). Values of NH$_4$ release at site 3 were significantly different from site 2 over all periods. At site 1, there were no significant differences between light and dark

Fig. 5 Fluxes of soluble reactive phosphorus (SRP) at (**a**) site 1 and (**b**) site 2, and fluxes of ammonium at (**c**) site 1 and (**d**) site 2 for light (L) and dark (D) benthic chambers for four periods of chamber deployment. Error bars represent standard errors ($n = 2$–4). For NH$_4$, dark bars represent initial release rates (0–12 h) and light bars represent secondary release rates (12–48 h)
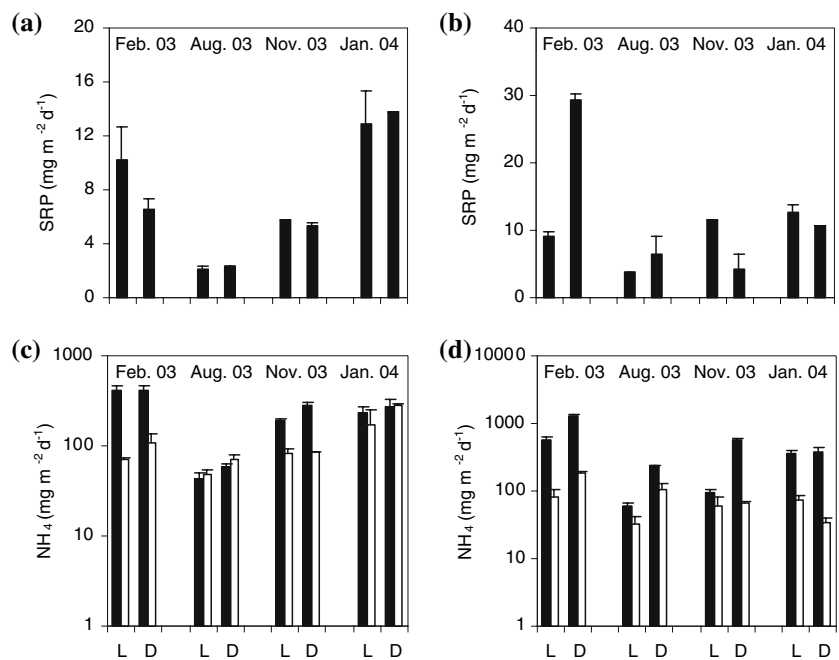
Table 4 Two way analyses of variance between period, chamber type (light or dark) and period × chamber for fluxes of soluble reactive phosphorus (SRP) and ammonium in the phase 0–12 h (NH₄ 1) and 12–48 h (NH₄ 2) at site 1 and site 2

Fluxes	Factor	Site 1				Site 2			
		df	MS	F	P	df	MS	F	P
SRP	Period	3	93	1.88	0.211	3	152	18.58	<0.01
	Chamber	1	7	0.14	0.722	1	44	5.36	0.05
	Period × Chamber	3	11	0.22	0.883	3	142	17.39	<0.01
	Error	8	49			8	8		
NH₄ 1	Period	3	88,717	30.81	<0.01	3	259,983	56.58	<0.01
	Chamber	1	4,824	1.68	0.232	1	810,886	176.48	<0.01
	Period × Chamber	3	1,464	0.51	0.687	3	240,907	52.43	<0.01
	Error	8	2,880			8	4,595		
NH₄ 2	Period	3	22,754	12.55	<0.01	3	71,205	9.93	<0.01
	Chamber	1	7,899	4.36	0.070	1	72,473	10.11	0.01
	Period × Chamber	3	2,410	1.33	0.331	3	60,865	8.49	<0.01
	Error	8	1,813			8	7,170		

df is degrees of freedom, MS is mean squares, F is the test statistic and P is probability

chambers for both phases of NH₄ release. At site 2, initial rates of NH₄ release were significantly higher ($P < 0.05$) in dark chambers than in light chambers.

Discussion

Sediment nutrient fluxes

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

Sediment release rates of SRP remained relatively invariant through time in all chambers, irrespective of initial DO concentration or changes in DO. While SRP release rates are generally reported to be much higher during water column anoxia than under well-oxygenated conditions (Andersen & Ring, 1999; Nowlin et al., 2005), there is evidence in sediment core incubations for high release rates under aerobic conditions (Søndergaard 1989; Jensen & Andersen, 1992; Krivtsov et al., 2001). It has been suggested that SRP release under aerobic conditions is associated with high rates of organic material decomposition at the sediment-water interface (Marsden, 1989; Kleeberg & Kozerski, 1997). Rapid decomposition utilises oxygen and nitrate and may create localised reducing conditions leading to desorption of P from metal cation complexes (Kleeberg & Kozerski, 1997; Krivtsov et al., 2001).

Gächter et al. (1988) suggest that SRP release rates may also be partly controlled by changes in sediment microbial physiology, including uptake, storage and release of P, as well as production and decomposition of bacterial biomass. Rates of P sedimentation are high in Lake Rotorua (0.5–2.7 g TP m⁻² d⁻¹, Burger, 2006) and are therefore likely to be important in sustaining the high release rates observed in this study, particularly at the deeper sites. The large seasonal differences in release rates observed may be explained in part by changes in temperature, which controls rates of biological activity, as well as oxygen consumption rates and redox potential (Boström & Pattersson, 1982; Søndergaard, 1989; Søndergaard et al., 2003). Seasonal variability in sedimentation rates observed in the lake (Burger, 2006) may also be important.

A two-phase release rate was observed in the chamber incubations for NH_4. A sustained high initial rate of release in the first 12 h of chamber deployment was followed by a lower secondary release rate over the remaining 12 to 48 h. Increases in DIN concentration in sediment core incubations are typically found to be linear through time (Fukuhara & Sakamoto, 1988), although often only one measurement is collected following the first 24 h of incubation, which would not have captured the trends observed here. It is possible that our NH_4 fluxes may have been artificially enhanced by isolation of the sediments or disturbance of the porewaters during deployment, though there was no evidence of this phenomenon in association with SRP release. Further, the absence of NO_3 in the chambers suggests that nitrification did not occur or that if there was nitrification, the rate of denitrification was sufficiently rapid to rapidly remove NO_3. The release rate of NH_4 may have been associated with a decrease in bacterial metabolism and regeneration of NH_4 as the water column becomes progressively deoxygenated during each deployment. For example, before deployment of the chambers, high ammonium regeneration rates may be coupled to rapid nitrification and denitrification at the sediment–water interface. As DO decreases inside the chambers immediately after deployment, nitrification and denitrification may be shut down, leading to rapid build up of ammonium. Further, the secondary release rate observed in our chamber deployments may therefore represent the natural organic matter degradation rate normally observed under low DO. Without further experimental work involving artificial control of DO inside the chambers during incubations, it is difficult to ascertain the exact mechanisms leading to the high variability of ammonium release observed over time within chambers.

Release rates of NH_4 of up to 2,212 mg m^{-2} d^{-1} estimated in this study are also much higher than those observed elsewhere. In a literature review of NH_4 release rates in freshwater systems, Hargreaves (1998) lists a highest value of 185 mg m^{-2} d^{-1} while Fukuhara & Sakamoto (1988) found dissolved inorganic nitrogen (DIN) release rates of between 0.7 and 240 mg m^{-2} d^{-1}.

Previous sediment release estimates for Lake Rotorua of 250–530 mg NH_4 m^{-2} d^{-1} (White et al., 1978), based on changes in hypolimnion concentration during a stratification event, were within the range observed here. High rates of NH_4 release have been found to coincide with high organic matter sedimentation rates (Fukuhara & Sakamoto, 1988) and in Lake Rotorua, sedimentation rates of up to 228 mg TN m^{-2} d^{-1} have been observed, with rates increasing significantly with increasing water column depth (Burger, 2006). The lack of a significant difference in sediment SRP and NH_4 release rates between light and dark benthic chambers at site 1 suggests that primary productivity at the sediment water interface may not have an important influence in mediating nutrient fluxes in shallow regions, perhaps as a result of high rates of advective transport and sediment disturbance not allowing an opportunity for significant accumulation of periphyton biomass. By contrast, at intermediate depths where there are high rates of deposition of chlorophyll (Burger, 2006), there may still be sufficient light for production and respiration by benthic algae to influence nutrient uptake rates between light and dark chambers (e.g. Dodds, 2003). For example, despite very low light levels at site 2 (< 1% of surface irradiance), rates of SRP and NH_4 release, and SOD were all lower in light than in dark chambers.

Verification of rates

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

Table 5 Source and description of nutrient load components used in Fig. 6

Component	Reference	Period	Method
External nutrient load	Burger, 2006	Jan. 01–Dec. 03	Daily loads associated with 9 major, 17 minor and ungauged inflows, and rainfall
Sedimentation rates	Burger, 2006	Feb. 03–Jan. 04	Sediment trap deployments coinciding with chamber deployments in this study
Outflows	Beyá et al., 2005	Jan. 02–Dec. 02	Monthly nutrient loads in single outflow
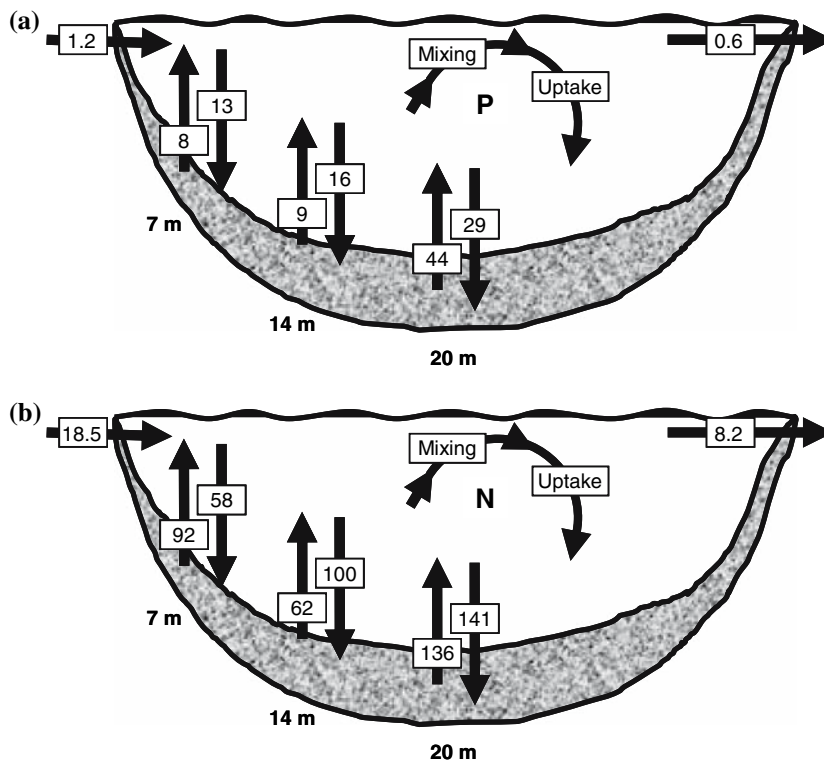
Fig. 6 Cycling of (**a**) phosphorus and (**b**) nitrogen in Lake Rotorua. All units are expressed as aerial rates (mg m^{-2} d^{-1}). Inflow, outflow and sedimentation rates represent total concentrations (TP or TN) and sediment release rates represent soluble reactive phosphorus (SRP) or ammonium (NH$_4$, secondary release rate). Sedimentation and sediment release rates are expressed as a seasonal mean calculated over the four sampling periods. Inflow and outflow concentrations are derived from Burger (2006) and Beyá et al. (2005), respectively, and sedimentation rates are derived from Burger (2006). See Table 5 for sources of inflow, outflow and sedimentation rates

derived from our chamber measurements and those estimated using changes in hypolimnion concentration suggests that chamber measurements are indeed representative at the lake scale.

Hypolimnion NH$_4$ concentrations during the same stratification event in February 2003 increased from 0.046 to 0.291 mg L^{-1}, representing a mean release rate of 63.9 mg m^{-2} d^{-1} for bottom sediments below the thermocline. This rate is substantially lower than that estimated beneath the thermocline from the chamber deployments for the same period (131.2 mg m^{-2} d^{-1}), which was derived from the second rate of NH$_4$ release (12–48 h) observed in the light chambers and calculated as for SRP. However, estimates from the chambers do not incorporate loss of NH$_4$ due to nitrification, as may occur higher in the water column, or uptake by benthic organisms.

Internal verses external loads

Fluxes of nutrients in Lake Rotorua, based on data presented in Table 5, indicate that bottom sediments are the dominant source of N and P (Fig. 6). Mean SRP and NH_4 sediment release rates at all sites, calculated from the current study, were at least three times greater than the mean daily external load determined by Burger (2006, Table 5). Mean release rates of SRP at site 3 exceeded mean TP sedimentation rates at the same site (Burger, 2006, Table 5), indicating the importance of the deeper sediments as a source of SRP to the water column. The fluxes did not include estimates of porewater SRP and NH_4 remobilisation in the shallow regions of the lake due to resuspension, or releases of dissolved organic phosphorus and dissolved organic nitrogen, that would have resulted in elevation of TP and TN releases above those measured for SRP and NH_4 Rates of water column denitrification, which may have important implications for the loss of N from the lake, were also not measured in the present study.

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

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