

# Retention of nitrogen, phosphorus and silicon in a large semi-arid riverine lake system

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**Abstract** Lakes and reservoirs (impoundments) are often viewed as a sink for nutrients within the river continuum. To date, most studies on nutrient retention within impoundments are derived from the temperate climate zones of Europe and North America, only consider one nutrient, and are often short-term (1–2 years). Here, we present a long-term (17 year) data set and nutrient (nitrogen, phosphorus and silica) budget for two connected semi-arid lakes (the Lower Lakes) at the terminus of the River Murray, Australia. Most of the filterable reactive phosphorus and nitrate entering the lakes were retained (77 and 92%, respectively). Total phosphorus (TP) was also strongly retained (55% of the annual TP load on average) and the annual TP retention rates could be predicted as a function of the areal hydraulic loading rate (annual lake outflow/lake surface area). On average, there was a slight net retention (7%) of the annual total nitrogen (TN) load but a slight net export (6% of the load) of organic N.

TN retention as function of the areal hydraulic loading rate was lower than expected from existing models, possibly because of high nitrogen fixation rates in the Lower Lakes. Silica was retained (39%) at similar rates to those observed in previous studies. There was also a marked increase in the TN:TP and TN:Si ratios within the lake (TN:TP ~ 30 and TN:Si ~ 0.67) compared to those entering (TN:TP ~ 15, TN:Si ~ 0.45), as a consequence of the relatively low net retention of nitrogen.

**Keywords** Nitrogen · Phosphorus · Silicon · Nutrient budget · Lake · Nitrogen fixation · Lake Alexandrina · Lake Albert · Stoichiometry · River Murray

## Introduction

Increased nutrient loading from anthropogenic sources and subsequent eutrophication are one of the greatest threats to aquatic ecosystems. The relationship between algal biomass and nutrient loading is now well established for estuarine and freshwater ecosystems (Howarth and Marino 2006). Anthropogenic activities also tend to modify the relative amounts of nutrients exported from catchments. In general, increased anthropogenic activity leads to a decrease in both the total nitrogen to total phosphorus (TP:TN) ratio (Caraco 1995; Howarth et al. 1995) and the

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dissolved silica to dissolved inorganic nitrogen (Si:DIN) ratio (Turner 2002). At TN:TP loading ratios <16 (mol:mol) there is an increased tendency for the development of blooms of cyanobacteria capable of nitrogen (N) fixation (Downing et al. 2001; Howarth et al. 1988a; Schindler et al. 2008; Smith and Bennett 1999). Similarly, Si:DIN ratios have been shown to exert an important control on the dominance of diatoms, with Si:DIN ratios <1 tending to favour the growth of flagellates over diatoms within coastal waters (Turner 2002).

Lakes and artificial impoundments (hereafter referred to as impoundments) are recognised as ‘hot spots’ within riverine systems for the trapping and cycling of nutrients. Virtually all studies to date have clearly shown that N, P and Si are strongly retained by impoundments and a number of models have been developed to describe their retention. Early work throughout the 1970s focused on P retention, reflecting the recognition that P was the limiting nutrient in most freshwater ecosystems (Howarth and Marino 2006). Numerous models of P retention have been developed, starting with the classic work of Vollenweider (Vollenweider 1969) and followed by numerous other studies recently summarised by Brett and Benjamin (Brett and Benjamin 2008). The more recent realisation that N plays a critical role in the eutrophication of coastal waters (Howarth and Marino 2006) has led to increased interest in the retention of N in impoundments (David et al. 2006; Harrison et al. 2009; Saunders and Kalff 2001). Relatively little work has been undertaken on Si retention by comparison to N and P, however, it has been clearly shown that a substantial fraction of Si can also be retained within impoundments (Humborg et al. 2006; Koszelnik and Tomaszek 2008; Triplett et al. 2008). The trapping of N and P by impoundments can generally be viewed as a positive attribute in the context of eutrophication, although we note that nutrient export from rivers, particularly in arid zones is crucial for the maintenance of coastal production (e.g., Gillanders and Kingsford 2002). The trapping of Si is generally viewed as a negative attribute because it is thought to lead to the preferential growth of flagellates over diatoms in coastal waters (Humborg et al. 2000). With the increasing recognition of nutrient stoichiometry in ecological function (Sterner and Elser 2002), it is surprising very few studies have simultaneously considered the

retention of N, P and Si within impoundments (Garnier et al. 1999).

Given that the TN:TP loading ratio can exert a strong influence over the abundance of N fixing cyanobacteria (Schindler et al. 2008), it seems reasonable to expect that the TN:TP loading ratio should also exert an influence on the N budget of impoundments. Numerous studies have shown that N fixation may be an important input of N to impoundments, particularly in arid and tropical systems (Ganf and Horne 1975; Horne and Galat 1985; Horne and Goldman 1972; Howarth et al. 1988b). To date, only one study has shown that lakes with high populations of cyanobacteria may actually be a net exporter of N, and this was in a subtropical reservoir with a low N:P (~1:1 mol:mol) loading ratio (Ashton 1981). Despite a relatively large number of nutrient budgets for temperate impoundments (Harrison et al. 2009; Saunders and Kalff 2001; Seitzinger et al. 2002; Tomaszek and Koszelnik 2003), there are no reports of net N export, even in those with blooms of N fixing cyanobacteria (Noges et al. 1998) and N:P loading ratios below 10 mol:mol (Galicka 1992; Galicka and Penczak 1989). It has been observed that areal N fixation rates tend to be higher in arid and subtropical aquatic ecosystems, than in temperate ecosystems, owing to the relatively short growing seasons in temperate regions (Grimm and Petrone 1997; Howarth et al. 1988b). We hypothesise that in arid and subtropical climates N fixation will be an important part of N budgets of riverine impoundments, N fixation will be high at low TN:TP loading ratios (<16) and ultimately lead to reduced N retention in impoundments.

Here we present a long term data set from a shallow semi-arid set of lakes at the terminus of Australia’s largest river system, the River Murray. We use this data to construct budgets for N, P and Si and to assess their relative retention and whether a lake in a semi-arid climate retains N to the same extent as that documented in temperate climates.

## Methods

### Study site

A detailed description of the Lower Lakes has previously been given in the literature (Geddes 1984;

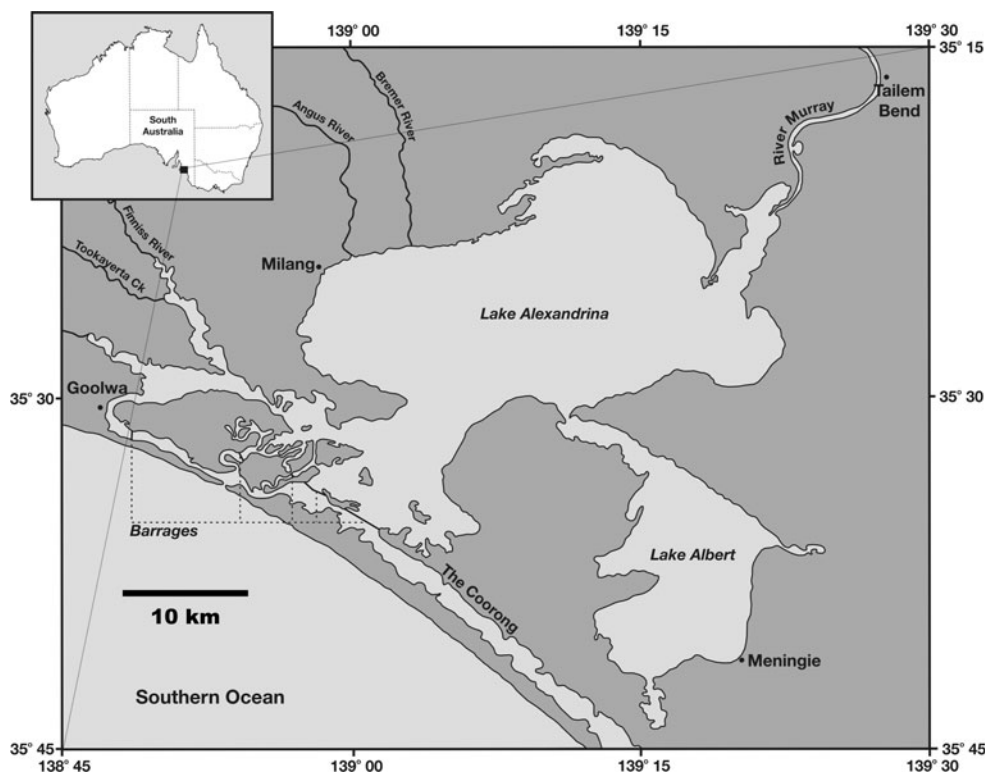
Geddes 1988). The Lower Lakes are situated at the terminus of the Murray-Darling Basin and the River Murray, Australia's largest drainage basin (1,063,000 km<sup>2</sup>) and one of the world's longest rivers (Newman 2000). Due to diversions for irrigation, annual runoff from the river is now <27% of that pre-European settlement, peak runoff is in early summer (when peak demands for irrigation occur) and the frequency and duration of small and medium floods has decreased significantly (Jolly 1996). The Lower Lakes are large (mean area  $\sim 8.0 \times 10^8$  m<sup>2</sup>), shallow lakes (maximum depth of 4.1 m) and the temperature ranges between an average minimum of  $\sim 10^\circ\text{C}$  in winter up to an average maximum of  $22^\circ\text{C}$  in summer (Sims and Muller 2004). Although several local streams discharge into Lake Alexandrina (Fig. 1), their overall contribution to total annual flow are only considered to be significant during periods of low River Murray inputs (Anon 2007). To prevent sea water intrusions in the Lower Lakes, five dams (hereafter referred to as 'barrages') were constructed between 1935 and 1940 to maintain the lakes as a

permanent freshwater supply for irrigation and human use (Fig. 1).

Lake Alexandrina and Lake Albert have suffered from the regular occurrence of cyanobacterial blooms (including species capable of N fixation), particularly during periods of low flow and low turbidity (P. Baker, Australian Water Quality Centre, "personal communication"). In fact, it was the site of the first record of a toxic bloom of cyanobacteria (*Nodularia spumigena*) in Australia (Francis 1878). Furthermore, pico-cyanobacterial (e.g. *Aphanocapsa*, *Planktolyngbya*) blooms now occur annually, blooms of *Nodularia spumigena*, *Anabaena circinalis* *Aphanizomenon/Anabaena* are common and the first recorded bloom of *Cylindrospermopsis raciborskii* occurred in the lakes in 2006 (P. Baker, "personal communication").

#### Sample collection and analysis

Surface water grab samples from the Lower Lakes (Milang) and the River Murray (Tailem Bend, Fig. 1)



**Fig. 1** Location on the Lower Lakes and associated localities where samples were collected

were typically collected 1–4 times per month by the Australian Water Quality Centre (AWQC). Water samples from ephemeral tributaries to the Lower Lakes in the Eastern Mount Lofty Ranges were collected sporadically by the Environment Protection Authority (EPA, South Australia) and the South Australian Department of Water, Land and Biodiversity Conservation (DWLBC).

All water samples were analysed by the AWQC, a National Association of Testing Authorities accredited laboratory using standard colorimetric methods. The parameters considered in this study were, nitrate + nitrite ( $\text{NO}_x$ ), silica (Si, molybdenum reactive fraction), total Kjeldahl nitrogen (TKN), filterable reactive phosphorus (FRP) and total phosphorus (TP) because they were the parameters consistently covered at both sites. Total nitrogen (TN) concentrations were calculated as  $\text{TKN} + \text{NO}_x$ . Only the years 1979–1996 were considered as this was the most comprehensive period of water quality data collection. Where monthly data were missing (occasionally at Milang in the years 1979–81) the concentration for the missing months was taken as an average of the preceding and subsequent months. This was justified on the basis that there was little variability in the analytes up to and subsequent to the missing data. Analytes below their detection limits ( $\text{NO}_x$ , FRP, and Si) were assumed to have half the concentration of the detection limit for budgeting purposes. Detection limits for nutrients were  $\text{NO}_x$  0.4  $\mu\text{M}$ , FRP 0.1  $\mu\text{M}$ , TP 0.1  $\mu\text{M}$ , TKN 3.5  $\mu\text{M}$  and Si (silica) 35  $\mu\text{M}$ . Samples for  $\text{NO}_x$ , FRP and Si were filtered through 0.45  $\mu\text{m}$  membrane filters upon collection and stored frozen, and samples for TP and TKN remained unfiltered and were stored frozen before digestion.

#### Load calculations and lake budget

Annual nutrient retention in the Lower Lakes was calculated as

$$M_{\text{ret}} = M_{\text{in}} + M_{\text{atm}} - M_{\text{bar}} - M_{\text{irr}} \quad (1)$$

where  $M_{\text{ret}}$  is annual retention,  $M_{\text{in}}$  is the annual load into the lakes from the River Murray and the small streams draining the Eastern Mt Lofty Ranges,  $M_{\text{atm}}$  is annual atmospheric deposition,  $M_{\text{bar}}$  is the annual flow over the barrages, and  $M_{\text{irr}}$  is the annual load withdrawn by irrigation.

Estimates of the monthly inflows via the River Murray into the lakes at Wellington and outflows from the barrages were obtained from the Murray-Darling Basin Authority (MDBA) using the Murray-Darling Basin hydrological model BIGMOD (J. Davis, MDBA, “personal communication”). Nutrient loads into the lakes from the River Murray were calculated by multiplying the average monthly analyte concentration at Tailem Bend by the monthly inflow volume. Monthly loads were summed to obtain annual loads. A comparison of the loads obtained in this manner with more sophisticated approaches such as Kendall’s flow regime stratified ratio method (Kendall et al. 1983), gave identical results. Nutrient loads out of the Lower Lakes were calculated by multiplying the monthly outflow volume by the average monthly concentration of the analyte measured at Milang. Monthly loads were summed to obtain annual loads.

Nutrient concentration data were only sporadically available for the Finnis River, Bremer River and Currency Creek, which together account for 70% of the gauged flow from local streams (DWLBC, “unpublished data”). Consequently, loads were calculated from daily flow measurements and relationships obtained from flow-load regressions where adequate nutrient data existed. The final budget showed contribution of TN, TP and Si from these sources was the insignificant ( $\sim 1$ –2%) compared to total inputs to the Lower Lakes. As such, we made no attempt to scale up these estimates for all local stream inputs. This is consistent with the small amount of runoff produced by the local catchment when compared with River Murray inflows.

Irrigation withdrawal loads from the lakes were calculated by multiplying the mean annual concentration of the analyte at Milang by the estimated annual volume of water withdrawn for irrigation. Only annual data were available for irrigation withdrawals from the Lower Lakes spanning 1994–2004. Irrigation withdrawals were therefore estimated by taking the average of the annual withdrawals for the years 1994–2004, which was 31,000  $\text{ML year}^{-1}$  (1  $\text{ML} = 1000 \text{ m}^3$ ) with a standard deviation of 9000  $\text{ML year}^{-1}$  (DWLBC, “unpublished”).

Rates of atmospheric deposition were calculated from concentrations of  $\text{NO}_x$ , TKN, and FRP in rainwater measured at Adelaide airport (Wilkinson et al. 2006), multiplied by the surface area of the lake

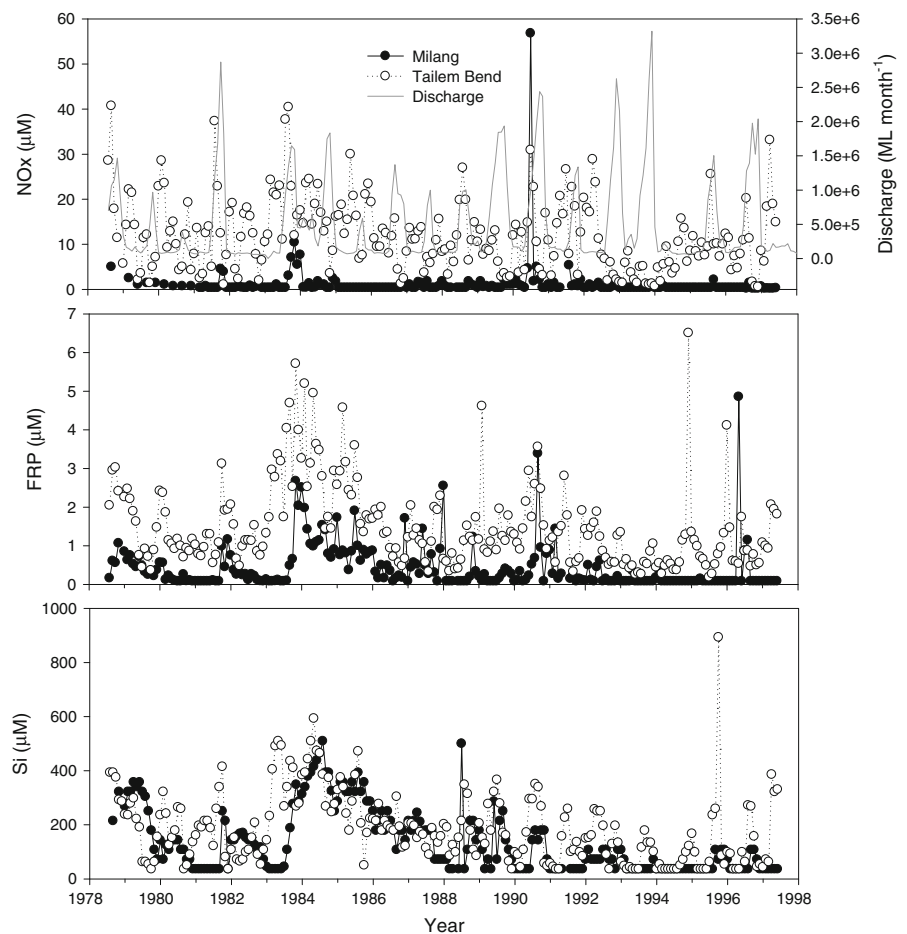
and annual average rainfall at Meningie (i.e. constant from year to year). This was justified on the basis of a strong dependence of nutrient deposition on times between rainfall events (i.e., more nutrients were deposited in rainfall events after a long dry period (Wilkinson et al. 2006)). Rates of dry deposition were not included for budgeting purposes for  $\text{NO}_x$  and FRP since these were unknown. Dry deposition rates for TKN were estimated to be 50% of wet deposition rates (Wilkinson et al. 2006). There is no information on TP deposition rates in the region, so we estimated a total annual atmospheric deposition rate of  $1 \text{ kg ha}^{-1} \text{ year}^{-1}$ , which is in the middle of the range of atmospheric deposition rates previously reported (Newman 1995). Inputs to the Lower Lakes from groundwater were ignored for the purposes of this budget since little relevant data exists for these potential inputs. The implications of not including this potential source are discussed later.

## Results

### Analyte concentrations in the River Murray and the Lower Lakes

Inorganic nutrient ( $\text{NO}_x$ , FRP and Si) concentrations were generally highest in the River Murray and decreased within the Lower Lakes, particularly  $\text{NO}_x$  and FRP (Fig. 2). Si concentrations showed a similar pattern, although this was less apparent. A drought-breaking inflow in late 1983 through to 1984 resulted in consistently high concentrations of all inorganic nutrients in the River Murray, which was also reflected in the Lower Lakes. Indeed, concentrations of Si and FRP remained elevated in the Lower Lakes and the River Murray for several years. By contrast,  $\text{NO}_x$  was rapidly removed from the water column, becoming undetectable within  $\sim 1$  year. The years 1989–1993 had consistently high flows, but elevated

**Fig. 2** Average monthly concentrations of  $\text{NO}_x$  (top panel), FRP (Filterable reactive phosphorus, middle panel) and Si (bottom panel) at Taillem Bend on the River Murray and Milang in the Lower Lakes. River discharge is also shown on the top panel, units are in megalitres ( $1 \text{ ML} = 1000 \text{ m}^3$ ) per month

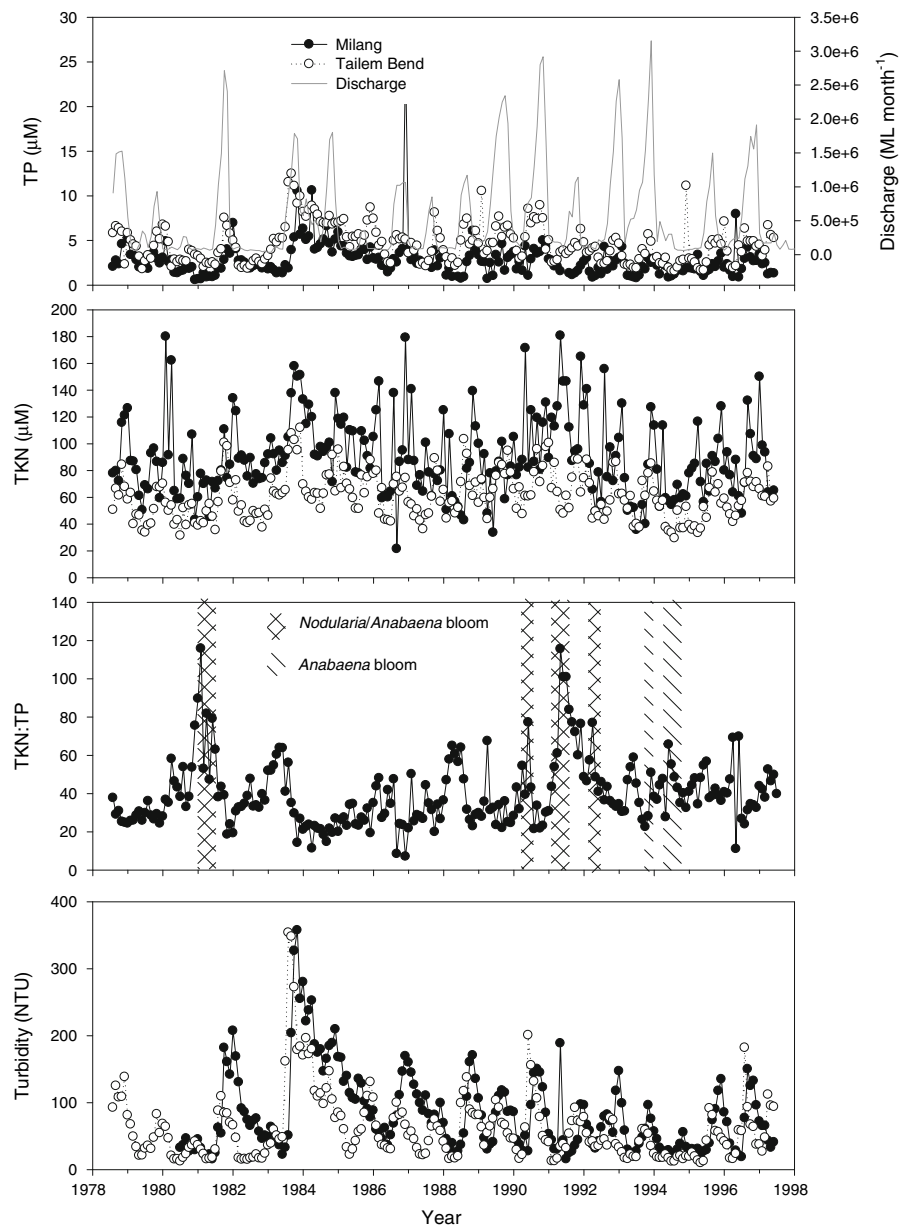


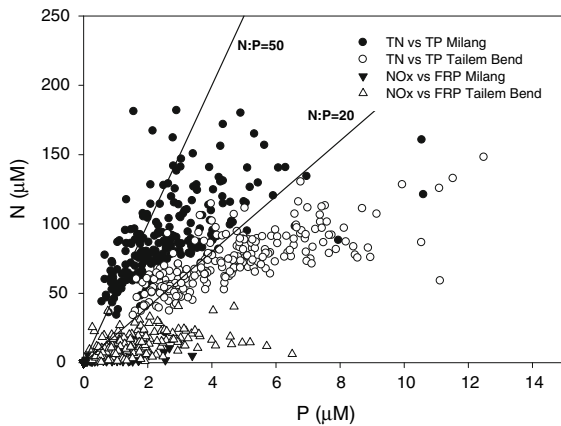
inorganic nutrient concentrations within the lake were only observed in 1990.  $\text{NH}_4^+$  was not determined on a routine basis, however, the limited data set available suggests it was always below the detection limit in the Lower Lakes and comprised a variable fraction (generally insignificant, but up to 50%) of inorganic N in the River Murray.

Total phosphorus concentrations were consistently highest in the River Murray and the highest concentrations in both the river and the Lower Lakes were associated with the drought-breaking

inflow event of 1983, as for the inorganic nutrients (Fig. 3). In contrast to TP and the inorganic nutrients, TKN concentrations (essentially organic N because of the low  $\text{NH}_4^+$  concentrations) were consistently highest in the Lower Lakes. The TKN:TP ratio was generally in excess of 20, increasing to in excess of 100 in 1983 and 1991 coincident with large blooms of *Nodularia spumigena* within the Lower Lakes (Geddes (1988); AWQC, “unpublished data”). There were also less pronounced peaks in the TKN:TP ratio coincident

**Fig. 3** Average monthly concentrations of TP (total phosphorus, *top panel*), TKN (total Kjeldahl nitrogen, *upper middle panel*), TKN:TP ratio (*lower middle panel*) and turbidity (*bottom panel*) at Tailem Bend on the River Murray and Milang in the Lower Lakes. River discharge is also shown on the *top panel*, units are in megalitres (1 ML = 1000 m<sup>3</sup>) per month. Marked areas indicate the occurrence of cyanobacterial blooms recorded within the Lower Lakes from 1990 onwards (Peter Baker, AWQC “personal communication”). The 1981 bloom was observed by Geddes (1988)





**Fig. 4** Plots of  $\text{NO}_x$  versus FRP (filterable reactive phosphorus) and TN (total nitrogen) versus TP (total phosphorus) for Taillem Bend on the River Murray and Milang on the Lower Lakes. Solid lines denote N:P ratios of 20 and 50 which denote the ratios below and above which N and P limitation are expected to occur respectively (Guildford and Hecky 2000)

with smaller *Anabaena circinalis* and *Nodularia* blooms in 1990, 1991 and 1993–1994 (based on cell counts, data not shown). In general, there was a clear increase in the TN:TP ratio from  $\sim 15$  in the River Murray, to  $\sim 30$  within the Lower Lakes (Fig. 4).

Turbidity in both the River Murray and the Lower Lakes was highly variable, but generally higher in the Lower Lakes than the River Murray. As was observed for the nutrients, the highest turbidity in the Lower Lakes was associated with the drought breaking 1983 inflow event. High turbidity in the Lower Lakes generally coincided with high turbidity in the inflowing water from the River Murray, with the notable exceptions of the austral summers of 1982/1983, 1986/1987 and 1992/1993, when high turbidity may have been caused by wind driven sediment re-suspension. The periods of lowest turbidity were always associated with periods of low flow, except for the occasional high value, as observed during the 1991 *Nodularia* bloom.

#### Nutrient retention in the Lower Lakes

Inorganic nutrients were generally strongly retained in the Lower Lakes with a net retention of  $\text{NO}_x$ , FRP and Si occurring virtually every year (Table 1). Highest absolute retention generally occurred in the highest flow years, whilst lowest absolute retention

rates occurred in the lowest flow years. Retention of  $\text{NO}_x$  (normalised to the mean lake surface area) ranged between 19 and  $200 \text{ mmol m}^{-2} \text{ year}^{-1}$  and generally, 90–100% of the  $\text{NO}_x$  entering the Lower Lakes was retained. For FRP, retention rates varied between 2.1 and  $33 \text{ mmol m}^{-2} \text{ year}^{-1}$ , with between 50 and 100% of FRP entering the Lower Lakes retained. Silica retention in the Lower Lakes was more variable, ranging from a slight source through to being a sink of  $2300 \text{ mmol m}^{-2} \text{ year}^{-1}$ . This represented an export equivalent to 39% of the incoming load and a retention of up to 92% of the incoming load. Retention of TKN was more variable, ranging from a net export of up to  $340 \text{ mmol m}^{-2} \text{ year}^{-1}$  (25% of incoming load) through to a net retention of  $190 \text{ mmol m}^{-2} \text{ year}^{-1}$  (35% of incoming load). There was a slight net export of TKN over the study period equivalent to 6% of the total incoming load. TN retention showed a very similar pattern to TKN, but there was a net balance in retention and export over the study period owing to the high retention efficiency of  $\text{NO}_x$ . TP was always retained, ranging between  $6 \text{ mmol m}^{-2} \text{ year}^{-1}$  in the lowest flow year of 1982, up to  $66 \text{ mmol m}^{-2} \text{ year}^{-1}$  in the high flow year of 1990. Retention of TP ranged between 27 and 98% of the incoming load, with an overall retention of 55% of the incoming TP over the 17 year study period. In general atmospheric deposition was  $<20\%$  of the Lower Lakes nutrient load, with the exceptions of the drought years 1982 and 1994, when atmospheric deposition was equivalent to 50 and 108% of the incoming TN and TP loads from the River Murray (data not shown).

#### Discussion

Whilst numerous nutrient mass balance studies of lakes have been carried out to date, this study is unique in a number of key respects. Firstly, this study reviewed nutrient retention within a semi-arid impoundment, which are hydrologically and ecologically significantly different from the more frequently studied temperate systems. Secondly, the patterns in N, P and Si retention were considered simultaneously. Finally, owing to a relatively long monitoring period, the patterns in nutrient retention between flood and drought periods in the River Murray could be compared. This is an important consideration

**Table 1** Annual inputs, outputs and net retention of nitrate + nitrite ( $\text{NO}_x$ ), filterable reactive phosphorus (FRP), total Kjeldahl nitrogen (TKN), total phosphorus (TP), Silica (Si) and total nitrogen (TN)

Year	Inputs						Outputs						Net retention									
	$\text{NO}_x$	FRP	TKN	TP	Si		$\text{NO}_x$	FRP	TKN	TP	Si		$\text{NO}_x$	FRP	TKN	TN	TP	Si				
												%										
1979	45	7	310	27	640	6.2	1.8	350	13	860	39	86	5.0	74	-38	-12	1.0	0.3	14	52	-230	-36
1980	27	3	110	9	300	0.6	0.1	53	1.3	100	26	98	3.0	98	59	53	85	62	8	86	200	66
1981	180	22	950	65	2800	27	4.7	850	27	1500	150	85	17	78	97	10	250	22	37	58	1300	46
1982	19	2	82	6	120	0.019	0.015	5.3	0.15	8.8	19	100	2.1	99	76	94	95	94	6	98	110	92
1983	220	36	900	95	3200	19	3.7	1100	29	910	200	91	33	90	-180	-20	20	1.8	66	70	2300	71
1984	170	31	870	90	4200	11	12	1100	54	3900	160	93	19	61	-200	-24	-40	-3.8	37	41	280	7
1985	38	6	190	16	510	0.20	0.90	120	4.2	380	38	99	4.9	85	70	38	110	47	12	74	130	25
1986	62	6	510	39	1300	1.7	3.0	660	28	1300	60	97	3.3	52	-160	-31	-100	-17	11	27	1.7	0.1
1987	43	5	240	18	580	2.0	1.4	200	5.9	460	41	95	3.6	71	46	19	87	31	12	67	120	21
1988	120	8	530	39	1500	2.60	0.67	350	10	920	120	98	7.2	91	190	35	310	48	28	73	600	40
1989	120	25	1400	110	3500	12	3.5	1200	45	2600	110	90	22	86	160	12	270	18	64	59	930	26
1990	190	37	1400	120	3400	27	15	1700	61	2200	160	86	22	61	-340	-25	-180	-11	61	50	1200	36
1991	85	6	490	28	680	8.0	0.92	520	7.2	87	77	91	5.1	85	-23	-4.7	54	9.4	21	75	590	87
1992	110	9	640	39	1200	4.9	0.98	630	18	550	110	96	7.7	89	2.1	0.34	110	15	21	54	690	56
1993	50	16	1300	82	1800	5.1	0.93	1600	45	900	45	90	15	94	-270	-21	-230	-17	37	45	910	50
1994	23	3	250	15	170	0.74	0.32	270	6.4	56	22	97	3.1	91	-26	-11	-4.0	-1.5	8	56	120	67
1995	100	4	430	29	1600	4.0	0.20	400	10	290	97	96	4.2	95	27	6	120	23	19	67	1300	82
1996	92	9	820	57	1500	3.7	3.2	950	30	600	88	96	6.0	65	-130	-16	-42	-4.6	27	47	910	60
Mean	94	13	630	49	1600	8.0	3.1	670	22	980	86	92	10	77	-36	-5.7	51	7.1	27	55	640	39

All values are in  $\text{mmol m}^{-2}$  lake area, except where % is indicated which denotes % of inputs retained. Negative values denote release from the lakes, positive values denote retention



because semi-arid rivers tend to have larger extremes in their water regime when compared to temperate river systems (Croke and Jakeman 2001). A significant fraction of the P and Si inputs were retained within the Lower Lakes. However, virtually no net N retention was observed over the 17 year study period and the lakes could be a small source of organic N. The potential hydrological and biogeochemical mechanisms responsible for this pattern in nutrient retention are now discussed.

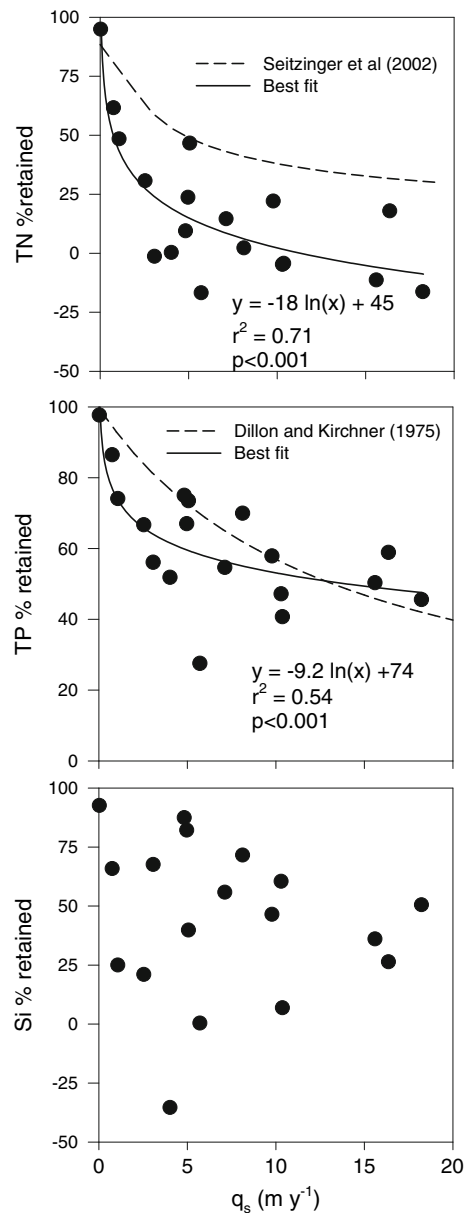
### Phosphorus

Phosphorus retention within lakes is most commonly described either as a function of the areal hydraulic loading rate (lake outflow/lake surface area) or the lake hydraulic residence time (lake volume/lake outflow). A recent comprehensive review of TP retention models showed that models formulated on hydraulic residence time are able to most accurately predict TP concentrations within lakes (Brett and Benjamin 2008). However, because hydraulic residence time models are weaker at predicting TP load retention (Kirchner and Dillon 1975), an areal hydraulic loading model was used here to describe N, P and Si retention in the Lower Lakes in common with other studies of waterbodies (e.g., Kadlec and Wallace 2009; Seitzinger et al. 2002).

There was a moderate relationship between the proportion of TP retained and the areal hydraulic load ( $q_s$ ) for the Lower Lakes, with a logarithmic function describing 54% of the variance (Fig. 5). For comparison, we have also shown a previously derived model for TP retention as a function of  $q_s$  (Dillon and Kirchner 1975):

$$R_p = v/(v + q_s)$$

where  $R_p$  is the proportion of P retained within the lake and  $v$  is the removal rate constant (often referred to as settling velocity). Using the average settling velocity of  $13.2 \text{ m year}^{-1}$  expected for North American and European lakes (Dillon and Kirchner 1975), this model tends to slightly over predict TP retention at low-intermediate  $q_s$  ( $<7 \text{ m year}^{-1}$ ), with better conformity at intermediate to high  $q_s$  ( $>7 \text{ m year}^{-1}$ , Fig. 5). The lower than expected TP retention rates at  $q_s < 7$  are probably caused by the shallowness of the lakes, which makes them prone to sediment re-suspension (Geddes 1984).



**Fig. 5** The proportions of total nitrogen (TN, *top panel*), total phosphorus (TP, *middle panel*) and Silica (Si, *bottom panel*) retained on an annual basis as a function of the areal water loading rate defined as the total annual outflow volume of the lake divided by the surface area. The dashed lines show a previously derived empirical model for TN retention (Seitzinger et al. 2002) and the equation  $\%TP \text{ retained} = v/(v + q_s)$ , where  $v = 13.2 \text{ m year}^{-1}$  for TP retention (Dillon & Kirchner 1975). The solid lines show the best fit to the data using a logarithmic function

The amount of TP retained within the lake between 1979 and 1996 amounted to an average of  $27 \text{ mmol m}^{-2} \text{ year}^{-1}$ . Based on an average sediment

TP content of  $250 \text{ mg kg}^{-1}$  dry weight and a sediment porosity of 0.65 (Aldridge et al. 2009), this amounts to an average sedimentation rate of  $\sim 4 \text{ mm year}^{-1}$  over the lake. This is in good agreement with a sedimentation rate of  $3 \text{ mm year}^{-1}$  calculated by Herczeg et al. (2001) in the Lower Lakes using  $^{210}\text{Pb}$ . As well as sedimentation, another possible sink for P is removal in the form of fish biomass by the commercial fisheries on the Lower Lakes. Using total fish catch data from the years 1985–1996 (South Australian Research and Development Institute, “unpublished data”) and assuming that P comprises  $25 \text{ g kg}^{-1}$  dry fish biomass, we estimate that fish biomass removal accounts for 2% of the total retention over the entire period 1985–1996. However, considerable variation was apparent, with calculated values ranging between 1 and 60%. The high proportion of 60% arose in the drought year 1994, when the mass of TP retained in the lake was negligible due to low TP inputs. The average estimated rate of P removal in fish biomass is somewhat lower than a rate of 10% estimated for Lake Donghu in China (Tang and Ping 2000).

## Nitrogen

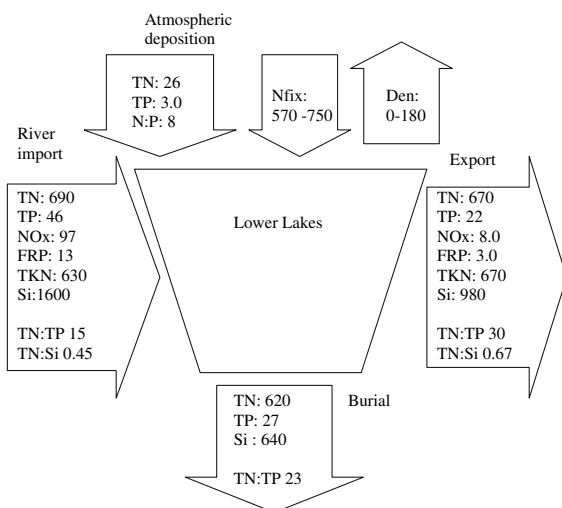
The retention of TN within the Lower Lakes was generally much lower than that observed in other studies (Seitzinger et al. 2002), particularly at areal hydraulic loading rates of  $5\text{--}20 \text{ m year}^{-1}$ . In fact, there was often an observed net export of N from the Lower Lakes (Fig. 5). This is quite unusual, with the only other reported instance of net annual N export that we could find occurring in the Rietvlei dam in South Africa (Ashton 1981). In that instance, high rates of N fixation were directly measured in the dam and were of a similar magnitude to the net export of N. While there are no published rates of N fixation from the Lower Lakes, it seems reasonable to assume N fixation rates will be substantial, given the presence of several species of N fixing cyanobacteria. Further evidence for the occurrence of N fixation comes from inspection of water column data collected at Milang. There was often a continued drawdown of FRP after  $\text{NO}_x$  became undetectable in the water column (Fig. 2), suggesting severe N limitation, which one would normally expect to lead to a decrease in the TN:TP ratio to below 20 (Guildford and Hecky 2000). Despite this, the

TKN:TP ratio (in this case  $\text{TKN} \approx \text{TN}$ , because  $\text{NO}_x$  was always low or undetectable) virtually always remained above 20, and was often in excess of 100 when  $\text{NO}_x$  was undetectable (Fig. 3). The largest peaks in TKN:TP in 1980 and 1991 also coincided with documented blooms of *Nodularia spumigena* (Fig. 3). The net effect of this additional source of N was to substantially increase the TN:TP ratio in the Lower Lakes compared to that entering from the River Murray (Fig. 4). This observation is consistent with fertilisation experiments on Lake 227, where despite TN:TP loading ratios being reduced to  $<10$  (mol:mol), the TN:TP ratio within the lake remained  $>40$  as a consequence of N fixation by cyanobacteria (Schindler et al. 2008).

Based on the previously estimated sedimentation rate and a sediment TN content of 0.25% dry mass (Herczeg et al. 2001), we calculate a TN loss to the sediment of  $620 \text{ mmol m}^{-2} \text{ year}^{-1}$  for the Lower Lakes over the study period. Denitrification is also likely to be a sink for N within the Lower Lakes, however, we have no long term or widespread measurements of denitrification rates in this system. A synthesis of denitrification as a function of TN loading rate in a range of aquatic systems found that TN loading was a strong predictor of the denitrification rate ( $r^2 = 0.77$ ) and that  $\sim 25\%$  of the TN load was denitrified (Seitzinger et al. 2006). Based on this relationship and the measured annual average TN loading rate of  $720 \text{ mmol m}^{-2} \text{ year}^{-1}$  (Table 1), we calculate an average denitrification rate of  $\sim 180 \text{ mmol m}^{-2} \text{ year}^{-1}$ . There is, however, considerable uncertainty around this estimate of denitrification for several reasons. Firstly, the regression that this estimate is based on, is derived predominantly from North American and European systems, in which,  $\text{NO}_x$  generally comprises  $>40\%$  of TN loads (David et al. 2006; Galicka and Penczak 1989; Howarth et al. 1996; Noges et al. 1998) compared to 13% of TN loads to the Lower Lakes. Given that  $\text{NO}_x$  concentrations exert a strong control over denitrification (Seitzinger 1988), one would expect much higher removal rates of N in impoundments where  $\text{NO}_x$  is the dominant fraction of TN. In this regard, our estimate may be an over estimate. Secondly, as discussed below, there is likely to be a substantial amount of extra N loading to the Lower Lakes through N fixation, which is not taken into account in the above estimate of denitrification. In this

regard our estimate of denitrification may be an underestimate.

A mass balance of TN losses (export, burial and denitrification) with known TN sources (river import and atmospheric deposition) is complicated by the fact that we have a highly uncertain estimate of denitrification. Assuming no denitrification takes place, leaves a minimum deficit of  $570 \text{ mmol m}^{-2} \text{ year}^{-1}$ . Including our above estimate of denitrification leaves a deficit of  $\sim 750 \text{ mmol m}^{-2} \text{ year}^{-1}$ . We, therefore, conservatively estimate a minimum TN deficit in the range  $570\text{--}750 \text{ mmol m}^{-2} \text{ year}^{-1}$  which we ascribe to N fixation as previously discussed (Fig. 6). A comparison of this deficit with previously reported N fixation rates shows it is well above the rate of  $\sim 120\text{--}140 \text{ mmol m}^{-2} \text{ year}^{-1}$  previously reported for desert lakes (Horne and Galat 1985; Horne and Goldman 1972). It also overlaps the high end of the range of  $360\text{--}650 \text{ mmol m}^{-2} \text{ year}^{-1}$  previously reported for eutrophic tropical and subtropical lakes (Ashton 1981; Ganf and Horne 1975; Horne and Viner 1971). Viewed another way, the deficit of  $570\text{--}750 \text{ mmol m}^{-2} \text{ year}^{-1}$  is roughly equivalent to the TN load into the Lower Lakes from the River



**Fig. 6** An approximate budget for N and P in the Lower Lakes spanning the years 1979–1996. Quantities shown are the average annual rate normalised to the surface area of the lake over the 17 year study period with units in  $\text{mmol m}^{-2} \text{ year}^{-1}$ . TN denotes total nitrogen, TP denotes total phosphorus, FRP denotes filterable reactive phosphorus, TKN denotes total Kjeldahl nitrogen, Den denotes denitrification and Nfix denotes nitrogen fixation. Please refer to discussion section ‘nitrogen’ for details of how nitrogen fixation and denitrification were estimated

Murray which is consistent with previous estimates of N fixation contributing on the order of 50% to total inputs to lakes in arid and tropical systems (Ashton 1981; Horne and Galat 1985; Horne and Goldman 1972; Horne and Viner 1971). Thus, while the rates of N fixation required to meet our budget deficit are high, they are plausible based on previous studies.

The finding that the Lower Lakes consumed  $\text{NO}_x$  and were a slight source of TKN contrasts with a review of the biogeochemistry of N and P in Australian catchments (Harris 2001). One of the main conclusions of that study was that Australian lakes and reservoirs consume TKN and DON and release  $\text{NO}_x$ . The mechanism behind our observations was most likely the assimilation of  $\text{NO}_x$  by phytoplankton to form biomass (TKN) as well as loss through denitrification. We ascribe this discrepancy to the fact that the lakes reviewed by Harris (2001) were deeper and that the water released was generally bottom water. As such, these waters would have been much more aphotic than those in the current study, leading to the dominance of organic matter mineralisation rather than production through photosynthesis.

## Silicon

In contrast to N and P, the proportion of Si retained within the Lower Lakes showed no clear relationship with the areal water loading (Fig. 5). There was a substantial retention of Si within the Lower Lakes over the study period, amounting to a total of  $\sim 40\%$  of the incoming load over the study period, which is consistent with a range of 40–60% estimated in previous studies (Garnier et al. 1999; Humborg et al. 2006).

## Stoichiometry of nutrient retention within the Lower Lakes

There is much interest in the interaction between nutrient ratios and ecological processes (Sterner and Elser 2002) and findings of this study provide a clear example of this on a landscape scale. The extremely low TN:TP loading ratio (TN:TP = 15 mol:mol) to the Lower Lakes, in combination with warm temperatures, were probably the major factors favouring the dominance of N fixing cyanobacteria (Downing et al. 2001; Howarth et al. 1988a; Schindler et al. 2008; Smith and Bennett 1999). Ensuing high rates of N

fixation resulted in a large increase in the TN:TP ratio of material leaving the lower lakes (TN:TP = 30, Fig. 6). These findings are consistent with the conclusion of Schindler et al. (2008) that any deficit in N availability relative to P will be made up through N fixation and that P loading was the ultimate control on algal biomass in this system. As such, we ascribe the low retention of N relative to P within the lower Lakes to the low TN:TP loading to the system. As a consequence, future models of N retention within impoundments may need to include the TN:TP loading ratio, particularly in tropical and arid regions to make them more globally applicable.

Si was also retained within the Lower Lakes much more efficiently than TN, resulting in the ratio of TN:Si ratio entering from the River Murray being increased from 0.45 to 0.67 over the entire study period (Fig. 6). It has been suggested that the trapping of Si by impoundments leads to a relative depletion in Si because anthropogenic activities replenish N and P, but not Si. The end result of this is an increase in flagellate blooms at the expense of diatoms (which have a high Si requirement) in coastal waters (Humborg et al. 2000). Whilst the Lower Lakes did reduce the amount of Si being released compared to TN, the TN:Si ratio exported from the Lower Lakes was still less than the ratio of  $\sim 1$  required for balanced diatom growth (Turner 2002). As such, even if all TN were to become bioavailable upon leaving the Lower Lakes (which is highly unlikely), Si would be unlikely to limit diatom growth within the river plume.

#### Budget approach and validity

One shortcoming of this study is that the concentrations used to calculate the loads out of the Lower Lakes were measured at Milang which is  $\sim 20$  km from the barrages. To assess the potential bias introduced by this we compared data from Milang with simultaneously collected data from Goolwa, located near one of the barrages (monthly,  $n = 85$ , years 1999–2006). Unfortunately, nutrients sampled at sites other than Milang were limited to  $\text{NO}_x$  and TKN, so our comparison is restricted to N.  $\text{NO}_x$  remained below the detection limit virtually at all times at Goolwa, confirming the uniform and rapid consumption of  $\text{NO}_x$  throughout the lakes. TKN concentrations were more variable with concentrations being slightly higher at

Milang (83  $\mu\text{M}$ ) than Goolwa (77  $\mu\text{M}$ ). However, these concentrations were not significantly different ( $t$ -test;  $p > 0.05$ ). Furthermore, as previously discussed there was excellent agreement between our estimates of TP retention over the study period and an independent estimate based on sediment P content and previously measured sedimentation rates. We are therefore confident that our budget approach yielded an accurate estimate of nutrient retention within the lakes.

Given the lack of spatial concentration data within the Lower Lakes, we also neglected changes in nutrient storage within the lakes. This may be a problem when interpreting data for a single year budget because a change in storage may be a significant proportion of the budget. Over the longer term, changes in storage are less of a problem, because years of net release will be tempered against years of net storage. We note that the water level in the Lower Lakes was kept at a relatively constant height and as such changes in volume from year to year were insignificant, except in the drought years 1982 and 1995, when the volume dropped by 15%. Thus, changes in storage will arise primarily as a consequence of changes in internal concentrations rather than changes in lake volume.

One possible source of N and P to the Lower Lakes that we have not considered in detail is groundwater since there is limited information available for the region. The discharge from the Angus Bremer Aquifer to the west is on the order of 3000 ML per year (Telfer et al. 2004). This is equivalent to 0.3% of the discharge of the River Murray in the lowest flow year, 1983, when the relative contribution from groundwater is likely to be highest. This aquifer is likely to be the source of the vast majority of groundwater discharge to the Lower Lakes, because it is recharged from the Mt Lofty ranges which have the highest annual rainfall in the region ( $\sim 600$ – $800$  mm per year compared to  $< 400$  mm on the surrounding plains; Australian Bureau of Meteorology). We assume this aquifer accounts for half the groundwater discharge into the Lower Lakes. There is no TN and TP concentration data available for the aquifers surrounding the Lower Lakes, however, the agricultural intensity is low and there is no reason to believe the concentrations of these nutrients are elevated. Using data from contaminated aquifers under regions of more intensive

agriculture 250 km to the South East (South Australian EPA, “unpublished data”), we calculate a TN and TP delivery equivalent to  $\sim 6\%$  and  $\sim 1\%$ , respectively, of the TN and TP entering the Lower Lakes from all other sources in the *lowest flow* year 1983. At this time the relative contribution from groundwater would be at its highest. Therefore, groundwater is unlikely to make a significant contribution to the TN and TP budget of the Lower Lakes.

## Summary and conclusions

The Lower Lakes were a substantial sink for  $\text{NO}_x$ , FRP, TP and Si, however there was relatively little retention of TN (Fig. 6). Consequently, there was a marked change in the TN:TP and TN:Si ratios of the loads exported from the Lower Lakes (TN:TP = 30, TN:Si = 0.67) compared to those entering (TN:TP = 15, TN:Si = 0.45). TP retention generally conformed to existing models derived from temperate lakes in Europe and North America. N, by contrast, showed much lower retention rates than expected from previously derived models in Europe and North America. We suggest the low N retention within the Lower Lakes was caused by high rates of N fixation by cyanobacteria, in agreement with previous studies of arid and subtropical lakes. Models for N retention in lakes outside the temperate regions for which most current models are derived, should therefore be based on empirical data derived from the region of interest. The models should also consider the N:P loading ratios which may exert a strong influence over N retention within lakes when the TN:TP loading ratio drops below  $\sim 16$  (mol:mol).

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