

Department of Primary Industries

**Gippsland Lakes Future Directions and Actions Plan:
Task E3.7: Assessment of the importance
of sediment-bound nutrients**

Andrew R. Longmore

Simon Roberts¹

Brett Light²

Marine and Freshwater Systems

Primary Industries Research Victoria

¹**School of Evolutionary Biology, Monash University**

²**Environment Protection Authority**

Internal Report No. xx

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July 2003

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Summary

The Gippsland Lakes is subject to frequent, severe blooms of the cyanobacterium *Nodularia spumigena*, which may have ecological, economic and human health impacts. Algal blooms depend on nutrients, which may be supplied from the catchment, or from internal stores in the sediments. The calibration of a predictive model of bloom response to catchment inputs in the Gippsland Lakes was based, in part, on nutrient fluxes measured at only three deep sites. An NHT-funded study indicated that nutrient fluxes differ greatly between deep (>5 m) and shallow (<3 m) waters, but was based on work in only three seasons. The Gippsland Lakes Future Directions and Actions Plan provided support to allow completion of a fourth seasonal survey of nutrient fluxes in deep and shallow waters. The work was carried out to achieve the following outcomes:

- (1) Measurement of spatial and temporal changes in fluxes
- (2) Assessment of the total release of nutrients from sediments
- (3) Assessment of the relative importance of sediment nutrients in contributing to algal blooms
- (4) Identification of the areas and conditions under which sediment nutrient release is most likely to occur.

Spatial differences were larger than seasonal differences in benthic nutrient fluxes. Average inorganic nitrogen and phosphate fluxes were four times higher at the deeper sites than at the shallower sites. Reasons for the spatial differences may include differences in the supply of organic matter, dissolved oxygen concentrations, active uptake of nutrients by microphytobenthos, or the effects of fauna associated with shallow waters. When shallow and deep-water fluxes are extrapolated to the whole of the surface area of the Gippsland Lakes, the annual nutrient input from the sediments is larger than the catchment input. Fluxes from the deeper waters for as little as 10 days would be sufficient to supply the nitrogen and phosphorus requirements of a large bloom. These data suggest that, particularly in years of low river flow, the internal nutrient loading could be the most significant source for primary producers. Western Lake Victoria comprises only 11% of the surface area of the Lakes, but supplies more than 50% of the nitrogen and phosphorus fluxes. Phosphate fluxes vary with the supply of organic matter, and bottom-water oxygen concentration, both factors taken into account in the CSIRO model. In contrast, we found that inorganic nitrogen fluxes depended much more strongly on the carbon supply than on oxygen concentrations. It may be that the CSIRO model would reproduce observations more closely if the dependence within the model of nitrogen processes on ambient oxygen concentration was removed.

Overall fluxes in the Gippsland Lakes are dominated by those from the deeper waters, and incorporating shallow-water processes into the existing model based on deep water fluxes would be an enhancement, rather than a fundamental change. The CSIRO model predicts low algal biomass in dry years, suggesting that catchment inputs are the key driver of blooms. Simple calculations here indicate that benthic fluxes could provide enough nutrients, even in a dry year, to drive a large bloom. If these are both true, it suggests that *Nodularia* blooms depend on a catchment input other than nutrient (e.g. a fall in salinity, trace growth factor) to trigger a bloom. If so, nutrient reductions from the catchment may not reduce algal bloom size or frequency. Research recently completed, and more underway into bloom triggers may help to clarify this point.

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1 Introduction

The Gippsland Lakes is subject to frequent, severe blooms of the cyanobacterium *Nodularia spumigena*, which may have ecological, economic and human health impacts. Amongst many factors, cyanobacterial blooms require large supplies of nutrients. While the ultimate source of nutrients to an estuary is the catchment, there is increasing evidence that recycling from the sediments may be a significant nutrient source in the Gippsland Lakes (Longmore 1990; Longmore 1994; Longmore 2000; Longmore *et al.* 2001; Roberts *et al.* 2003). Calibration of the sediment module of the CSIRO biogeochemical model for the Gippsland Lakes (CSIRO 2001) was based on such evidence, which was drawn principally from the deeper areas of the Lakes. Plants, which are restricted to the shallower areas of the Lakes, may substantially alter benthic nutrient recycling processes (Sundback *et al.* 1991). Failure to include the impact of plants in the shallower areas may lead to errors in the CSIRO model calibration, and therefore in the subsequent uses of the model to generate tests of various management scenarios. In particular, deficiencies in model simulation of benthic nutrient recycling would lead to greater uncertainty in predictions of the rate and extent of change to algal blooms expected from reductions in catchment nutrient inputs.

The Natural Heritage Trust funded a 12-month study to assess the importance of sediment-released nutrients in fuelling algal blooms in the Gippsland Lakes. The collaborative project between Monash University, EPA, MAFRI and GCB involved sampling at eight sites (four shallow, four deep) for benthic nutrient fluxes on four occasions over 7 months. The conceptual model underlying this approach is shown below (Fig 1). In this model, nutrients entering the Lakes, from the rivers, creeks, drains, groundwater, Bass Strait and the atmosphere are taken up by phytoplankton. Grazing by zooplankton leads to some recycling of nutrients in the water column, but a significant proportion of the nutrients bound in phytoplankton eventually fall to the sediment surface. Some of the organically bound nutrients are buried in the sediment, while the rest are broken down by microbial activity in the near-surface sediments. Microbial activity results in the conversion of nutrients from particulate organic forms into more biologically available dissolved inorganic forms, which accumulate in the sediment or are transported back into the water column. The chemical species, thus formed, depend on the microbial pathways involved. These processes are modified by other plant forms (e.g. seagrasses, macroalgae, microphytobenthos on the sediment surface) and by the activity of animals living on and in the sediment.

Roberts *et al.* (2003), on the basis of fieldwork in three seasons, concluded that fluxes at shallow (< 2 m) sites were substantially lower than at the deeper (> 5 m) sites. While the deep site sediments appeared to be consistent sources of nutrients, the shallow sites could either be sources or sinks. Unfortunately, NHT required the project to be completed before summer sampling could be carried out. Summer sampling was needed to provide a complete seasonal study. Extra funding, which was required for the summer sampling, was provided as part of the wider Nutrients and Sediments (A5) and Planning, Monitoring and Evaluation (E3) components of the Gippsland Lakes Future Directions and Actions Statement.

The project was designed to provide:

1. A measure of the spatial and temporal changes in sediment nutrient flux in the Gippsland Lakes;
2. An assessment of the total release of nutrients from sediments in the Gippsland lakes;
3. An assessment of the relative importance of the sediment nutrients in contributing to algal blooms;
4. Identification of the areas and conditions under which sediment nutrient release is most likely to occur in the Gippsland Lakes.

Assessment of the importance of sediment-bound nutrients

It was also intended to lead to the verification (or rejection) of the assumed links in the CSIRO model between water quality, nutrient release and algal blooms, and advice which could lead to subsequent refinement (if necessary) of the CSIRO model.

The sampling was carried out in February 2003, and this report, in conjunction to the NHT report (Roberts *et al.* 2003), completes the project.

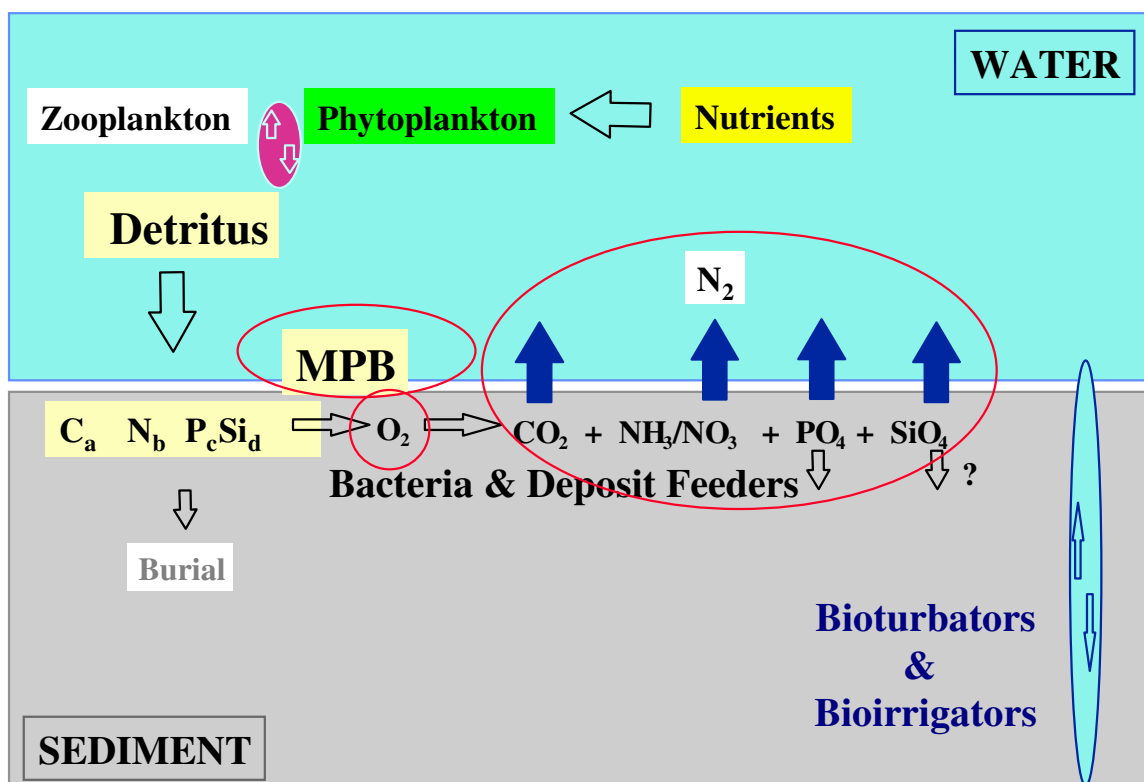


Figure 1 A process model for Gippsland Lakes nutrient cycling. The processes monitored at the sediment surface in this program are circled in red. The MPB (microphytobenthos) compartment also includes other aquatic vegetation.

2 Methods

The methods involved have been detailed in Roberts *et al.* (2003). Briefly, eight sites were sampled, four in shallow waters, and four in deep waters (Fig 2). All sites were sampled with transparent benthic chambers, using *in situ* light fields. Benthic chambers trap a known volume of water over a known area of sediment, and we follow the change in concentration of oxygen, carbon dioxide and nutrients in the chamber over time, as they are consumed by, or released from, the sediment. Shallow sites were sampled with up to four replicate chambers during daylight, while the deeper sites were sampled by one chamber each during the day and again overnight. Shallow sites were also sampled by up to six smaller chambers, designed to continuously measure the impact of microphytobenthos on oxygen concentration.

Assessment of the importance of sediment-bound nutrients

Fluxes were estimated by linear regression of nutrient concentration with time, and extrapolated from the period of incubation to a daily rate.

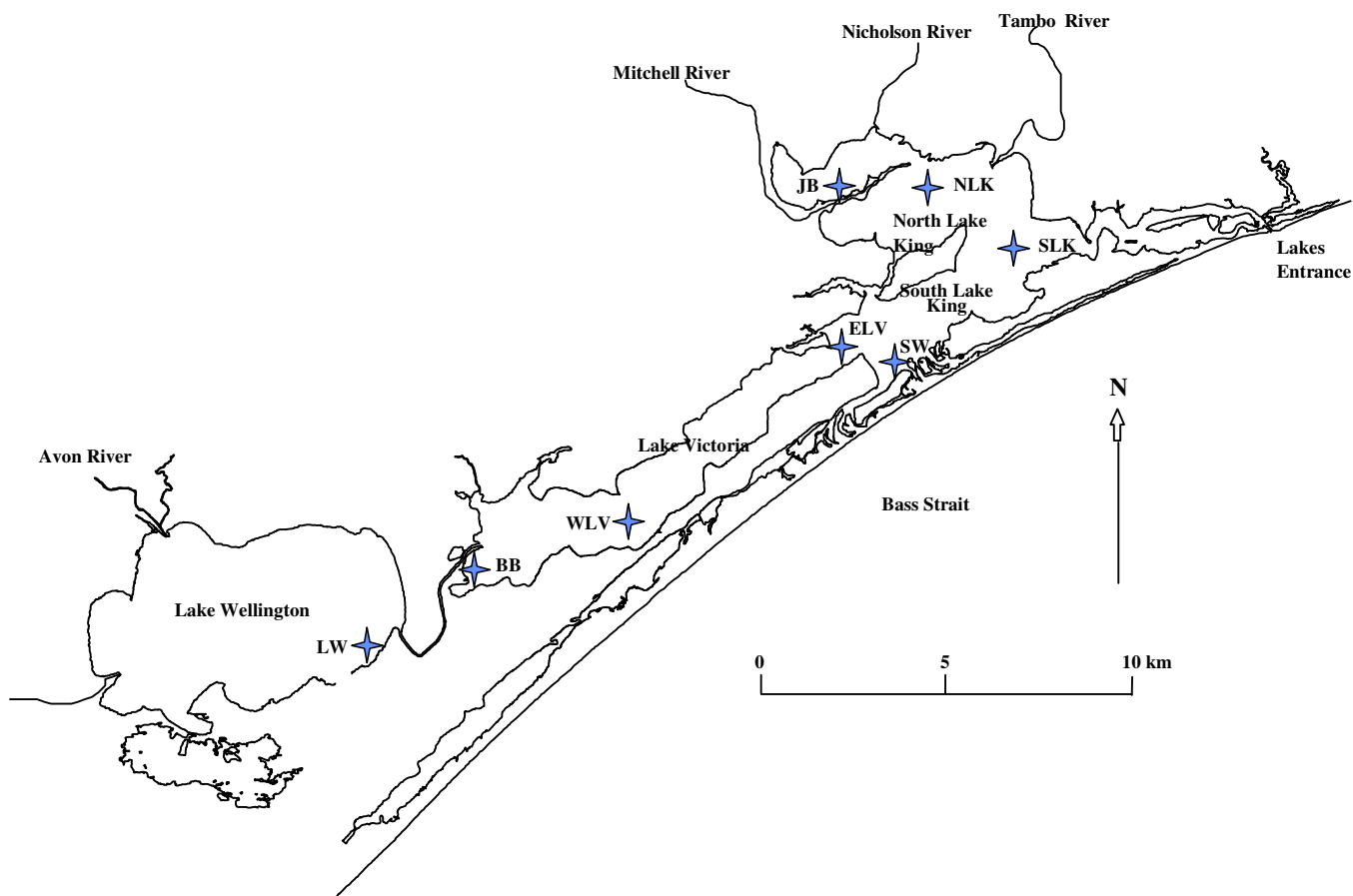


Figure 2 Sampling sites. Shallow sites were in Jones Bay (JB), Spermwhale Head (SW), Bandin Bay (BB) and Lake Wellington (LW). Deep sites were in North Lake King (NLK), South Lake King (SLK), East lake Victoria (ELV) and West Lake Victoria (WLW).

3 Results

3.1 Deep sites

Benthic fluxes from the deep sites in February 2003 varied significantly with location, but also between replicate chambers (Table 1). The single largest C, N and P fluxes were measured at the northern Lake King site. Mean dissolved inorganic nitrogen fluxes were similar ($5.8\text{--}6.9\text{ mmol N m}^{-2}\text{ d}^{-1}$) at three sites, and lower ($1.47\text{ mmol N m}^{-2}\text{ d}^{-1}$) in south Lake King. Phosphate fluxes varied in the same manner ($0.48\text{--}0.94\text{ mmol P m}^{-2}\text{ d}^{-1}$ at three sites, and $0.19\text{ mmol P m}^{-2}\text{ d}^{-1}$ in southern Lake King).

Table 1. Benthic fluxes measured in the deep sites in Gippsland Lakes, February 2003.

All fluxes $\text{m mol m}^{-2} \text{d}^{-1} \pm 1 \text{ S.E.}$, denitrification efficiency is %.

Flux	NLK	SLK	ELV	WLV	Mean
Day-time fluxes					
Dissolved oxygen	-43.9 ± 1.8	-31.0 ± 1.2	-67.5 ± 1.9	-29.0 ± 0.9	-42.9
Carbon dioxide	25.1 ± 1.7	22.1 ± 2.9	120 ± 7.8	106 ± 5.3	68.3
Ammonium	2.53 ± 0.22	2.06 ± 0.35	9.24 ± 1.2	9.76 ± 0.61	5.90
Nitrite	0.11 ± 0.02	0.16 ± 0.02	0.04 ± 0.00	0.07 ± 0.01	0.10
Nitrate	-0.02 ± 0.01	0.86 ± 0.37	0.04 ± 0.01	-0.02 ± 0.02	0.22
Phosphate	0.07 ± 0.01	0.15 ± 0.03	0.85 ± 0.13	1.23 ± 0.09	0.58
Silicate	3.83 ± 0.31	4.85 ± 0.42	13.5 ± 0.9	6.42 ± 0.60	7.15
N ₂	2.12 ± 0.16	2.04 ± 0.23	0.0 ± 0.0	2.42 ± 0.10	2.19
Denitrification efficiency	44.4 ± 4.0	42.9 ± 4.1	0.0 ± 0.0	19.8 ± 2.0	26.8
Night-time fluxes					
Dissolved oxygen	-84.4 ± 6.4	-49.4 ± 3.5	-42.4 ± 2.2	-51.5 ± 1.3	-56.9
Carbon dioxide	170 ± 17.6	47.9 ± 4.0	39.6 ± 3.1	71.8 ± 4.2	82.3
Ammonium	10.4 ± 1.2	0.67 ± 0.14	2.28 ± 0.18	3.87 ± 0.24	4.31
Nitrite	0.08 ± 0.02	0.04 ± 0.00	0.04 ± 0.01	0.04 ± 0.00	0.05
Nitrate	0.03 ± 0.01	-0.02 ± 0.01	0.04 ± 0.01	-0.02 ± 0.01	0.01
Phosphate	0.89 ± 0.11	0.23 ± 0.03	0.30 ± 0.05	0.65 ± 0.08	0.52
Silicate	10.8 ± 1.3	3.20 ± 0.27	8.15 ± 0.54	4.38 ± 0.49	6.63
N ₂	0.59 ± 0.05	1.29 ± 0.19	1.76 ± 0.16	0.69 ± 0.10	1.08
Denitrification efficiency	5.4 ± 1.0	65.1 ± 7.5	39.2 ± 4.6	13.7 ± 2.4	30.9

Table 2. Benthic fluxes measured in the shallow sites in Gippsland Lakes, February 2003.

All fluxes $\text{m mol m}^{-2} \text{d}^{-1} \pm 1 \text{ S.E.}$, denitrification efficiency is %.

Flux	LW	BB	SW	JB	Mean
Day-time fluxes					
Dissolved oxygen	21.7 ± 34.2	-27.6 ± 3.7	-64.6 ± 27.8	-8.4 ± 23.6	-19.7
Ammonium	1.24 ± 0.83	3.11 ± 2.27	0.97 ± 2.04	0.12 ± 0.15	1.36
Nitrite/Nitrate	0.32 ± 0.13	-0.11 ± 0.08	-0.10 ± 0.04	-0.05 ± 0.07	0.02
Phosphate	0.29 ± 0.08	0.17 ± 0.24	0.21 ± 0.25	-0.13 ± 0.10	0.14
N ₂		2.07 ± 1.82	4.08 ± 6.38		3.08
Denitrification efficiency		39.5 ± 13.0	55.9 ± 41.0		47.7
Dark fluxes					
Dissolved oxygen	-66.4 ± 33.5	-21.7 ± 6.7	-112.6 ± 8.7	-52.0 ± 19.9	-63.2

3.2 Shallow sites

Benthic fluxes in the shallow sites varied markedly between sites (Table 2). Dissolved inorganic nitrogen and phosphate fluxes were close to zero in Jones Bay, and much higher at the other three sites. Only one site (Lake Wellington) demonstrated net oxygen production during the day, and the balance of daytime and dark oxygen fluxes indicates that all four shallow sites would be net consumers of oxygen over a 24-hour period. Mean daytime oxygen fluxes were much lower than the dark fluxes (-19.7 compared to -63.2 mmol O₂ m⁻² d⁻¹). Average N and P fluxes were four times higher at the deeper sites than at the shallower sites.

4 Discussion

4.1 Spatial and temporal changes in sediment nutrient fluxes

4.1.1 Deep sites

For dissolved inorganic nitrogen and phosphate, distinct differences were observed between Lake King (low flux) and Lake Victoria (high flux, Figs 3-4). Also, west Lake Victoria fluxes were greater than east Lake Victoria fluxes. Though daytime oxygen consumption was lower than nighttime consumption at three of the deep sites, indicating some photosynthetic production, carbon dioxide production was lower in the day than night at two sites, and higher at the other two. Therefore we found no strong evidence of plant production in the deep sites, and sediments were net consumers of oxygen over a 24-hour period. Because the differences between replicate chamber incubations appeared to be unrelated to time of incubation (day/night), we attribute these differences to small-scale spatial variability. This variability presumably reflects small-scale differences in deposition of labile carbon. We conclude that we are probably justified in dividing the deeper waters into three zones (west Lake Victoria, east Lake Victoria and Lake King).

However, when averaged over all sites (Table 3), the seasonal differences in DIN and PO₄ fluxes were relatively small (4.2-6.1 N mmol m⁻² d⁻¹ and 0.5-0.8 mmol P m⁻² d⁻¹): the average was dominated by the west Lake Victoria site, where fluxes were always high. This is despite the mean carbon flux almost doubling from autumn to summer. Organic matter with a low C:N ratio is considered a richer food source than one with a higher C:N ratio. One interpretation of these observations is that the higher carbon fluxes in summer reflect increasing microbial activity, but that the microbes are consuming organic matter which is progressively poorer in nutrients, because river flow has been insufficient to stimulate large-scale primary production in the Lakes. An alternative view is that the higher carbon fluxes in summer reflect a higher supply of organic matter, but that its composition has changed (become poorer in nutrients) from autumn to summer. A shift in dominance from phytoplankton to seagrass could facilitate such a change.

Table 3. Deep site benthic fluxes averaged for each month.

All fluxes m mol m⁻² d⁻¹ ± 1 S.E., denitrification efficiency is %. C:N ratio includes DIN and N₂.

Month	CO ₂ flux	DIN flux	N ₂ flux	PO ₄ flux	C:N
May 2002	44.4	6.06	10.1	0.80	2.6
Aug 2002	56.6	6.13	5.0	0.76	4.8
Nov 2002	70.8	4.18	2.0	0.58	10.8
Feb 2003	75.3	5.34	1.4	0.55	11.8

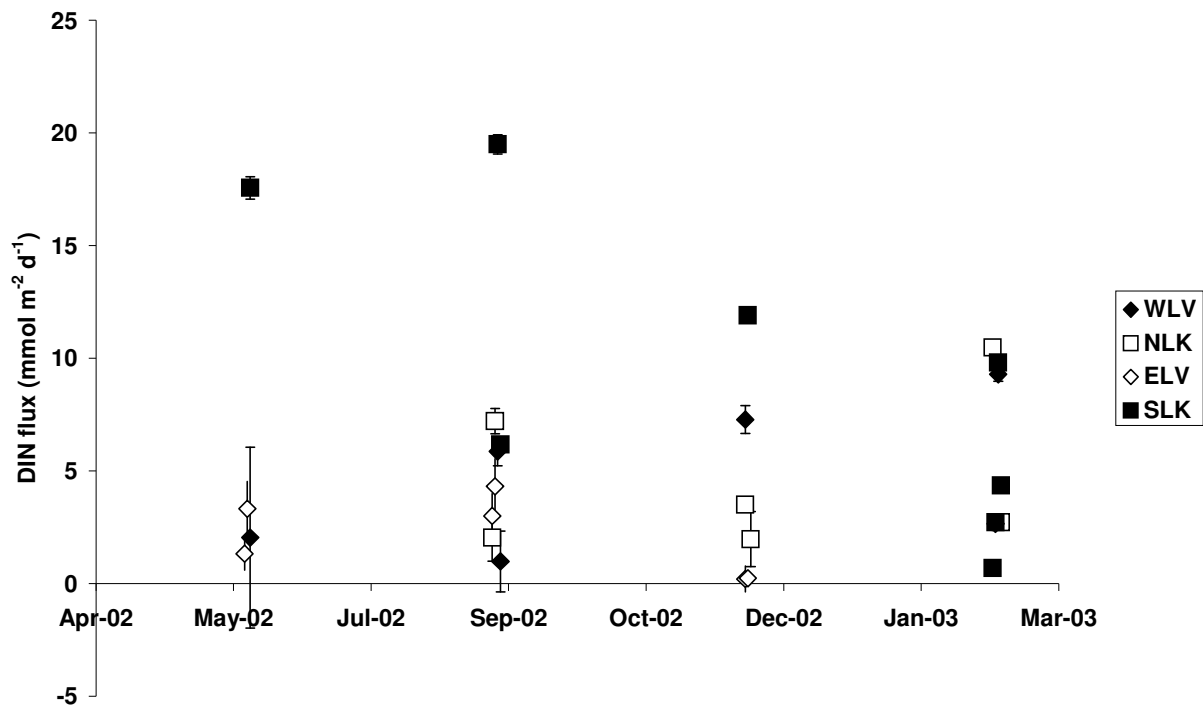


Figure 3 Dissolved inorganic N fluxes from all deep sites

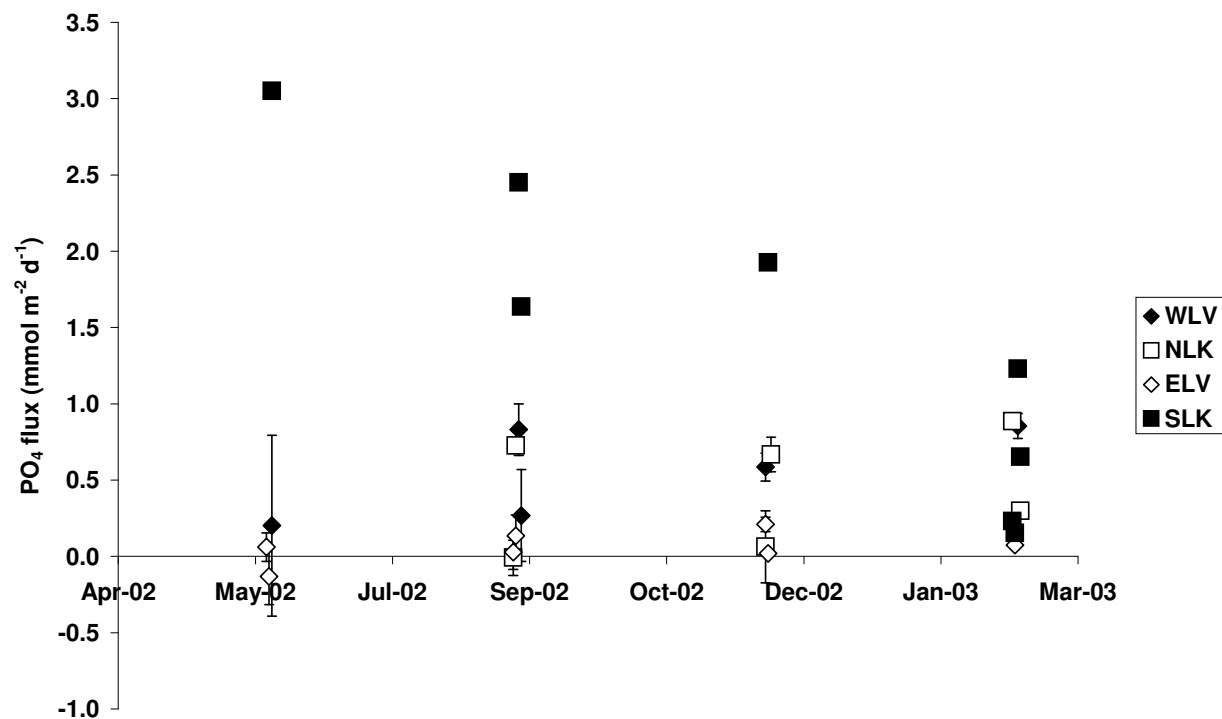


Figure 4 Phosphate fluxes from all deep sites

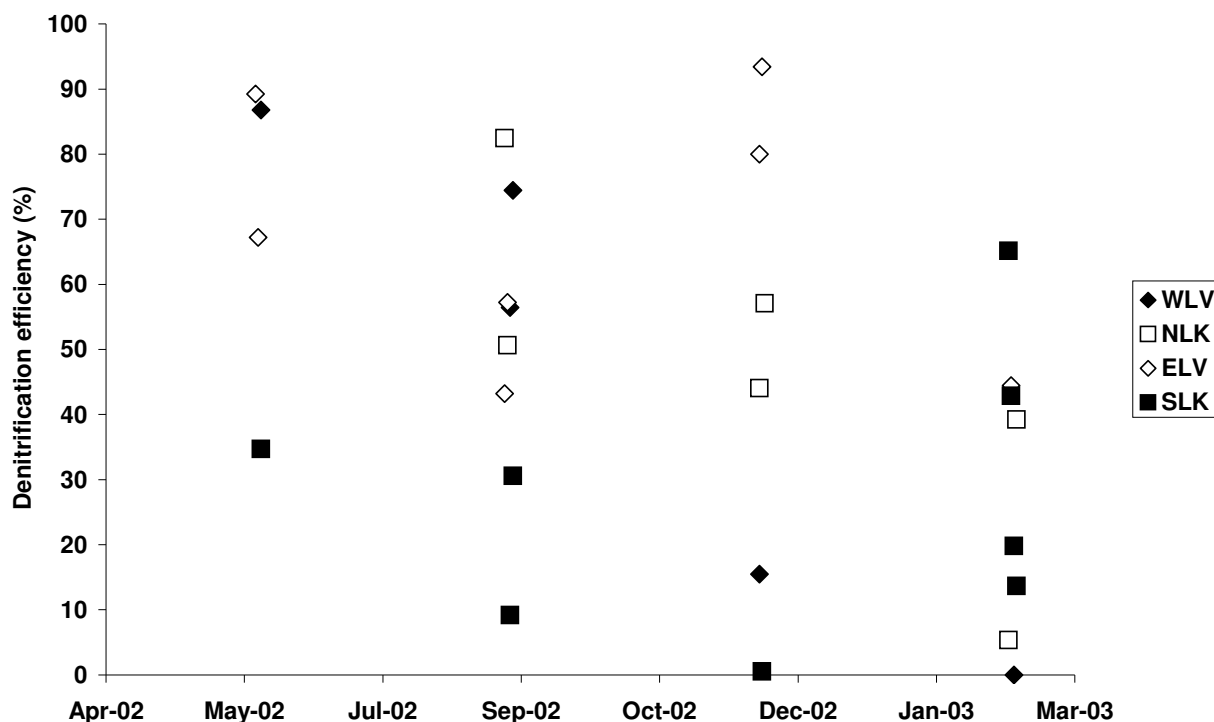


Figure 5 Denitrification efficiency from all deep sites

Denitrification efficiency is a measure of the effectiveness by which the sediments convert inorganic nutrients to N_2 gas, which is then lost to the atmosphere. If the growth of plants in a system is limited by nitrogen, high denitrification efficiency may help to prevent recycled nitrogen leading to algal blooms. Conversely, in a system with low denitrification efficiency, most of the nitrogen recycled from the sediments is in forms (ammonium, nitrate) readily available for plant growth. In the Gippsland lakes context, denitrification may be an important factor controlling blooms of diatoms and dinoflagellates, but it is likely to be less important in controlling cyanobacterial blooms such as *Nodularia*. This is because cyanobacteria have the capacity to fix N_2 gas, and are therefore more likely to be limited by phosphorus rather than nitrogen.

Over all seasons, denitrification efficiency was high in southern Lake King, low in western Lake Victoria, and variable at the other two sites (Fig 5).

4.1.2 Shallow sites

Mean oxygen fluxes were lower in light than dark incubations on all four sampling trips, indicating the effect of photosynthesis throughout the year at shallow sites. There was little seasonal change in ammonium fluxes at three of the shallow sites (Fig 6), with most fluxes close to zero. Bandin Bay was the exception. It generally had the highest flux of all four sites, and peaked in summer. Similarly, Bandin Bay had the highest phosphate fluxes in May and September 2002 (Fig 7), but in December 2002 and February 2003 was indistinguishable from the other three sites. Averaged over all four sites, the phosphate flux was close to zero, with a net release in May, September and February, and a net uptake in November.

Assessment of the importance of sediment-bound nutrients

We have therefore observed different seasonal patterns between ammonium and phosphate flux in the shallow sites, and in each flux between the shallow and deep sites. The differences in shallow sites arise mainly from the different behaviour of N and P in November in Bandin Bay. The net uptake of phosphate by sediments in November could indicate more efficient trapping of phosphorus in the near-surface oxic sediments by metal oxides at that time of year. This may be due to a seasonal increase in plant biomass leading to greater fluxes, offset by increased daylight oxygenation of the sediment surface, and hence more efficient P trapping. Ammonium is not trapped, and increased fluxes were observed in Bandin Bay in November.

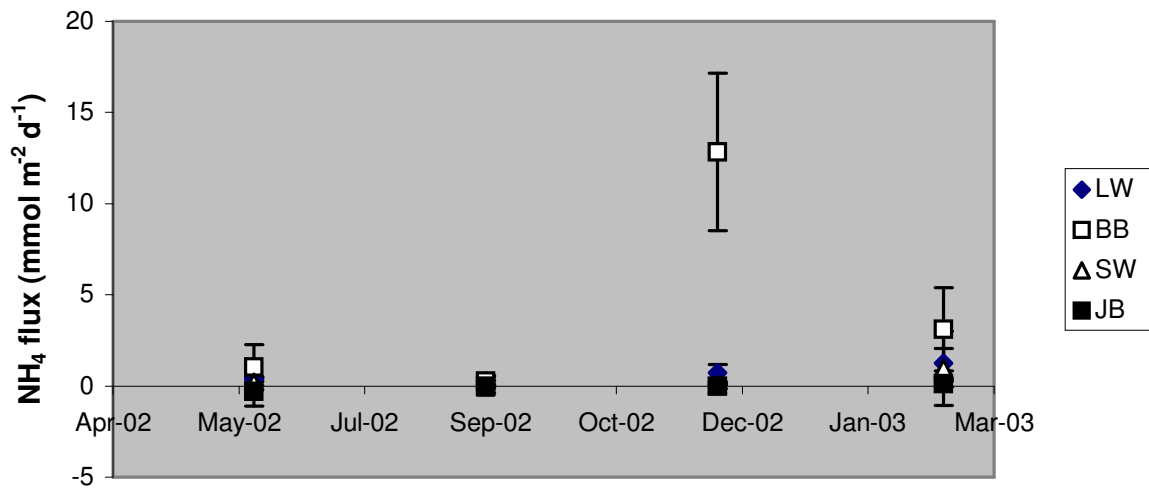


Figure 6 Dissolved inorganic NH₄ fluxes from all shallow sites

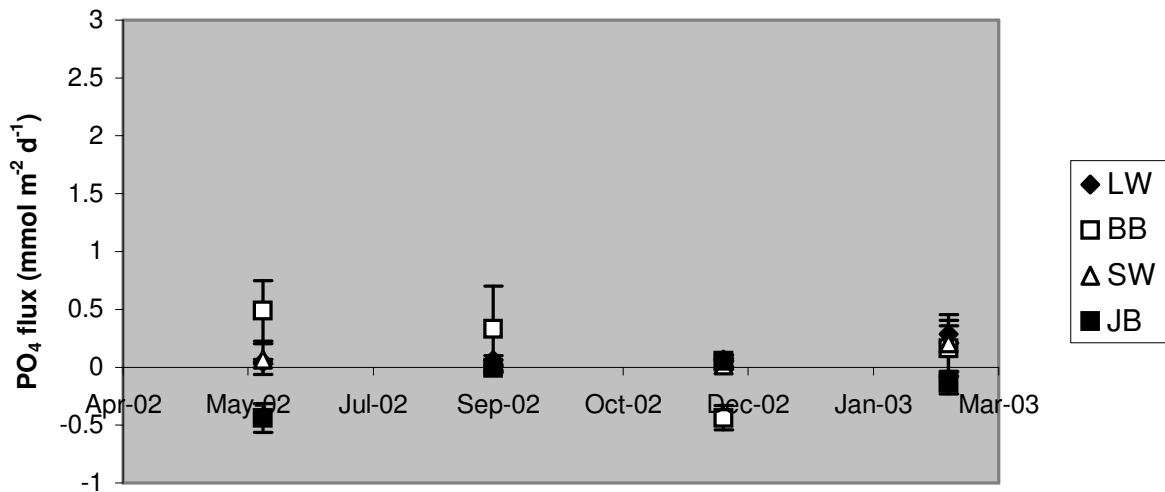


Figure 7 Phosphate fluxes from all shallow sites

The overall differences between shallow and deep sites could arise from several factors. These include differences in oxygen regime, carbon supply (net deposition, etc), efficient flux trapping by microphytobenthos and the influence of benthic animals. These factors are discussed in section 4.4.

4.2 Total release of nutrients from sediments

We can estimate the total dissolved inorganic nutrient flux from the sediments by making a number of assumptions:

- That each of the basins can be sub-divided into regions of differing flux on the basis of depth;
- That shallow and deep fluxes are representative of the end-members of the depth ranges;
- That fluxes at intermediate depths can be linearly interpolated from the shallow and deep end-members;
- That an annual flux can be estimated from the average fluxes of four quarterly surveys;
- That Bunga Arm, Reeves Channel and other shallow areas can be ignored.

When we assign representative areas to the data and multiply up for an annual flux (Table 4), the totals are of the same order of magnitude (though larger than) the 1977-1999 average catchment inputs estimated by Grayson *et al.* (2001). These data suggest that, particularly in years of low river flow, the internal nutrient loading could be the most significant source for primary producers. However, the intermediate depths, where there were no flux measurements, contribute significantly to these calculations. For example, extrapolations account for 75% of the area of Lake Wellington, 61% of Lake Victoria and 51% of Lake King. The extrapolation may therefore introduce a large margin of error, and indicate the need to measure fluxes at intermediate depths.

4.3 Importance of sediment nutrients to algal blooms

In this discussion, we will concentrate on those factors this study indicates are important to nitrogen (ammonium, nitrate and N₂) and phosphate fluxes. Figs 8, 9 and 10 together indicate that if the carbon supply could be kept below about 60 mmol m⁻² d⁻², then DIN fluxes could be kept below about 5 mmol m⁻² d⁻¹, phosphate fluxes could be kept below about 1 mmol m⁻² d⁻¹, and denitrification efficiency would be maintained at above 60%, levels approaching those found in Port Phillip Bay (Longmore and Gason 2001). However, even though they are low in relation to the range observed in the Lakes, such N and P fluxes would still be about five times higher than those found in Port Phillip Bay. Such nutrient release rates, over the deepest 20% of the Lake surface, would be sufficient over 10 days to supply all of the N and P required for a large bloom throughout the water column over an area of 100 km², equivalent to the whole of north and south Lake King (see Appendix 1 for calculation).

4.4 Areas and conditions under which sediment nutrient release is most likely

We have shown that the deeper sediments contribute substantially more per unit area than the shallower sediments. These differences may arise from differences between the depth zones in oxygen regime, carbon supply (net deposition, etc), or flux trapping by microphytobenthos.

Though we have no measurements to confirm it, we expect that the water column in the shallow regions is nearly always well-oxygenated, because there is a short pathway to the atmospheric oxygen supply, and also daylight production of oxygen by plants. In contrast, there is ample evidence (Longmore *et al.* 2001) that the deeper waters in the Lakes are often hypoxic (reduced oxygen concentrations) and sometimes anoxic (no oxygen). Anoxia prevents nitrification and denitrification proceeding, leading to the return of N to the water column as ammonium. Anoxia

Assessment of the importance of sediment-bound nutrients

also leads to the release of phosphate from metal oxides. We may therefore expect higher nutrient fluxes from the deeper waters.

Table 4. Estimated annual dissolved inorganic N and P release from sediments in the Gippsland Lakes, 2002-2003.

* Note: Intermediate depth fluxes are interpolated between shallow and deep fluxes, except in Lake Wellington, where no deep fluxes were measured.

Location	Depth range (m)	Area (km ²)	Mean DIN and PO ₄ flux (mmol m ⁻² d ⁻¹)	Mean DIN flux (tonnes N y ⁻¹)	Mean PO ₄ flux (tonnes P y ⁻¹)
Lake Wellington	<2	37	0.58, 0.06	110	25
	>2	111	0.58, 0.06*	330*	75*
West Lake Victoria	<2	9	5.1, 0.13	235	13
	2-4	14	7.27, 0.69*	520*	109*
	4-6	9	9.44, 1.26*	434*	128*
	>6	6	11.6, 1.82	356	123
East Lake Victoria	<2	9	0.16, 0.03	7	3
	2-4	14	1.7, 0.19*	119*	30*
	4-6	9	3.2, 0.35*	146*	35*
	>6	6	4.7, 0.51	144	34
Lake King	<2	36	-0.41, -0.13	-72	-52
(including Jones Bay)	2-4	34	0.83, -0.02*	144*	-8*
	4-6	26	2.1, 0.09*	274*	26*
	>6	21	3.1, 0.22	332	52
Total				3,079	593
Catchment inputs (ave 1977-1999)§				Tot N 2,800 DIN 1,040	Tot P 300 PO ₄ 105

§ Total catchment inputs from Grayson *et al.* (2001) have been multiplied by factors derived from Bek and Bruton (1979) to estimate the proportions of inorganic nutrients.

The question of differences in carbon supply between shallow and deep waters is more vexed. We could argue that there should be a higher carbon supply in deeper waters than shallow waters because the deeper waters are usually areas of deposition, while wave action may prevent deposition in shallower waters. A deeper water column may also host a larger phytoplankton biomass that contributes to the rain of organic matter to the sediments. On the other hand, shallow

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areas are host to most of the microphytobenthos, seagrasses and other plants. Despite the significant biomass of seagrass in the Gippsland Lakes, a biomarker survey (Longmore *et al.* 2001) did not identify seagrass residues in the deeper sediments. Seagrass blades presumably strand on the shore, and most of the recycling could take place there. While we can use carbon dioxide flux as a measure of organic matter supply in deep waters, we have no measure of the carbon dioxide flux in shallow waters. We could use oxygen flux as another estimate of carbon supply, but it is affected by photosynthesis in shallow waters and by lack of oxygen in deeper waters. Dark fluxes in November 2002 and February 2003, when deep oxygen concentrations were high, were similar in shallow and deep zones, suggesting that there were no major differences in the supply of carbon. It may be that differences in the sources of carbon between shallow and deep areas are the key. Shallow areas may be supplied by a range of plants, ranging from nutritionally rich, easily decomposed plants like microphytobenthos to plants like seagrasses that are nutrient-poor and resistant to decomposition. In contrast, the only supply of organic matter in the deeper waters may be nutritionally rich, easily decomposed phytoplankton. Under those circumstances, we may expect a higher flux of N and P per unit of carbon from deeper waters than from shallow waters.

The third factor to be considered is the impact the plants themselves may have on nutrient fluxes. Several studies (e.g. Sundback *et al.* 1991; Rysgaard *et al.* 1995) have demonstrated that microphytobenthos may modify benthic fluxes in at least two ways. The first is by intercepting nutrients from the sediments which are incorporated into biomass. The second is by increasing the oxygen concentration in surface sediments through photosynthesis, altering the balance of oxygen-sensitive processes and thereby promoting nitrification/denitrification and phosphorus trapping. Both processes would lead to a decrease in the net flux of nutrients from the sediments.

The last factor to be considered is the role infauna may play in benthic nutrient fluxes. Bio-irrigation by benthic infauna introduces oxygen deeper into the sediments than would otherwise be the case. Bio-irrigation may also enhance the escape into the water column of nutrients. A number of studies internationally have shown that bio-irrigation may lead to increases or decreases in denitrification efficiency, depending on size, number and spacing of burrows, oxygen content of water and rate of irrigation (Aller and Aller 1992; Mayer *et al.* 1995). Berelson *et al.* (1998) found that in Port Phillip Bay there was a weak negative correlation ($R^2 = 0.36$) between denitrification efficiency and rate of bio-irrigation. Nicholson *et al.* (1996) estimated that bio-irrigation enhanced ammonium fluxes 2-3 fold.

With our current knowledge, we are not able to favour one explanation above the others.

There are also differences in magnitude of fluxes between the basins. From Table 3, western Lake Victoria comprises only 11% of the surface area of the Lakes, but contributes 50% of the inorganic N flux, and 63% of the phosphate flux.

Given what we know of the factors governing phosphate release, and those affecting the processes of nitrification and denitrification, we may expect both carbon supply and bottom water oxygen concentration to influence nutrient fluxes and denitrification. DIN and phosphate fluxes, and denitrification efficiency from the deeper sites are strongly dependent on the carbon dioxide flux, which we take as a measure of the supply of labile carbon to the sediment (Figs 8-10). We may therefore expect greatest nutrient fluxes from sites of greatest deposition, which in general will be the deepest areas of the Lakes. While it may also include shallower, nearly land-locked areas (e.g. Newlands Arm, Box Creek) which have not yet been sampled for nutrient fluxes, most of these areas also have plant cover, and could be expected to behave like the shallow sites sampled in this study. That is, we expect them to contribute relatively little to net benthic fluxes.

Conversely, while there is a strong inverse relationship between phosphate flux and ambient oxygen concentration in the deep waters (Fig 11), DIN flux and denitrification efficiency appear to vary independently of ambient oxygen concentration (Figs 12,13). This is somewhat surprising, and at odds with both the theoretical basis of our understanding of the processes governing nitrogen recycling, and with the conclusions of a previous study in the Gippsland Lakes. Longmore *et al.*

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(2001) concluded (from measurements at three deep sites) that N and P benthic fluxes correlated better with bottom water oxygen concentrations than with carbon flux.

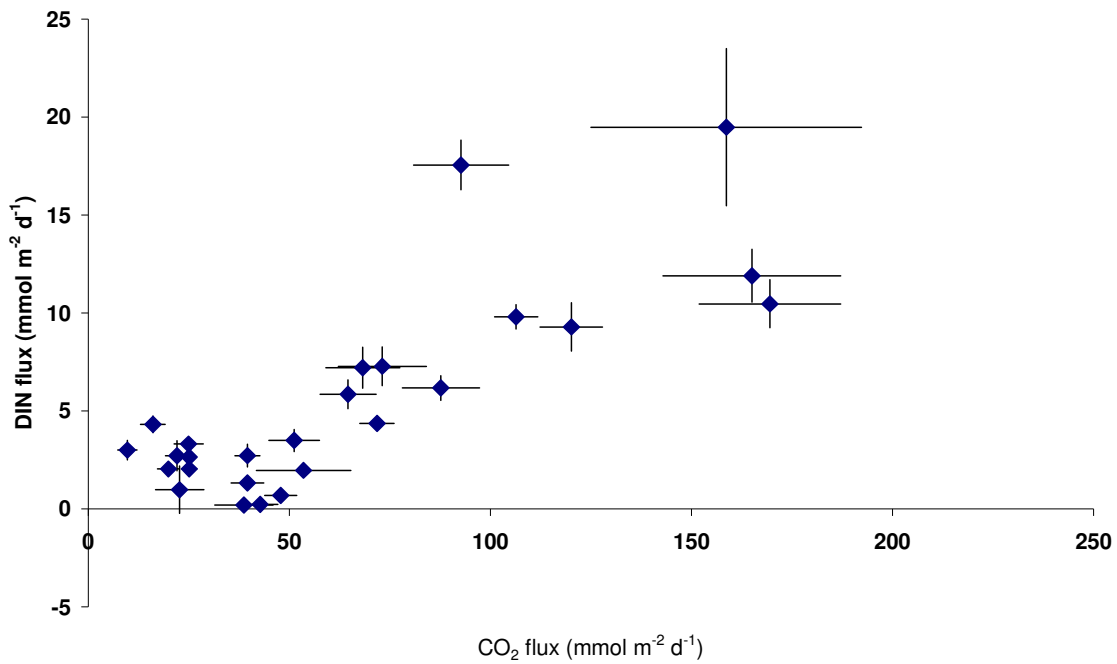


Figure 8 Variation of DIN flux with carbon supply in deep sites

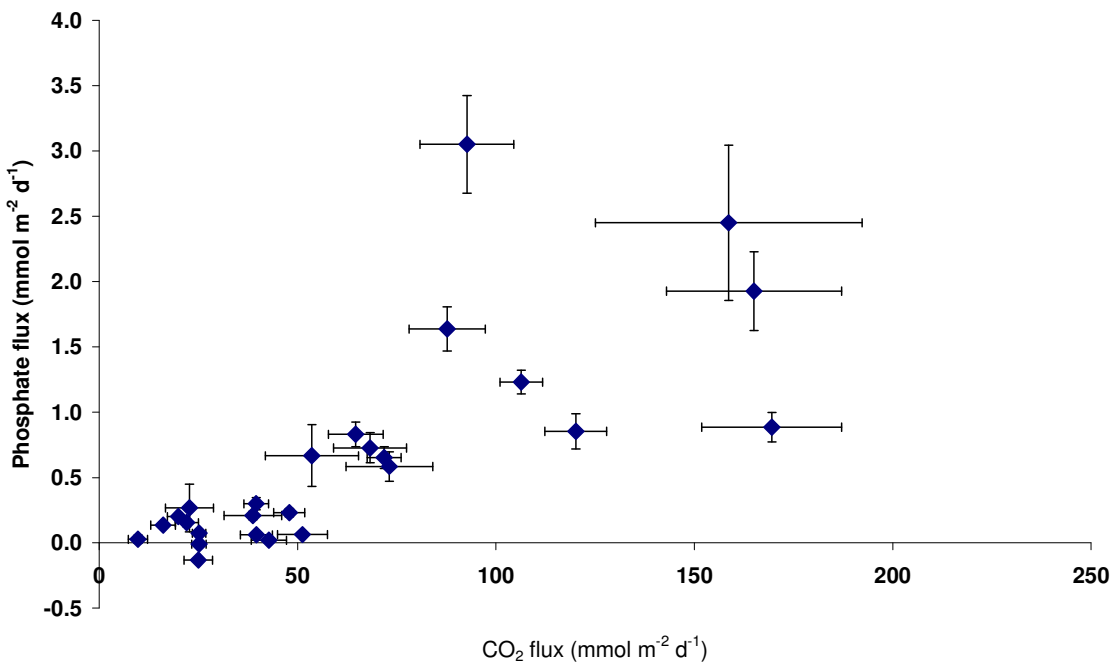


Figure 9 Variation of phosphate flux with carbon supply in deep sites

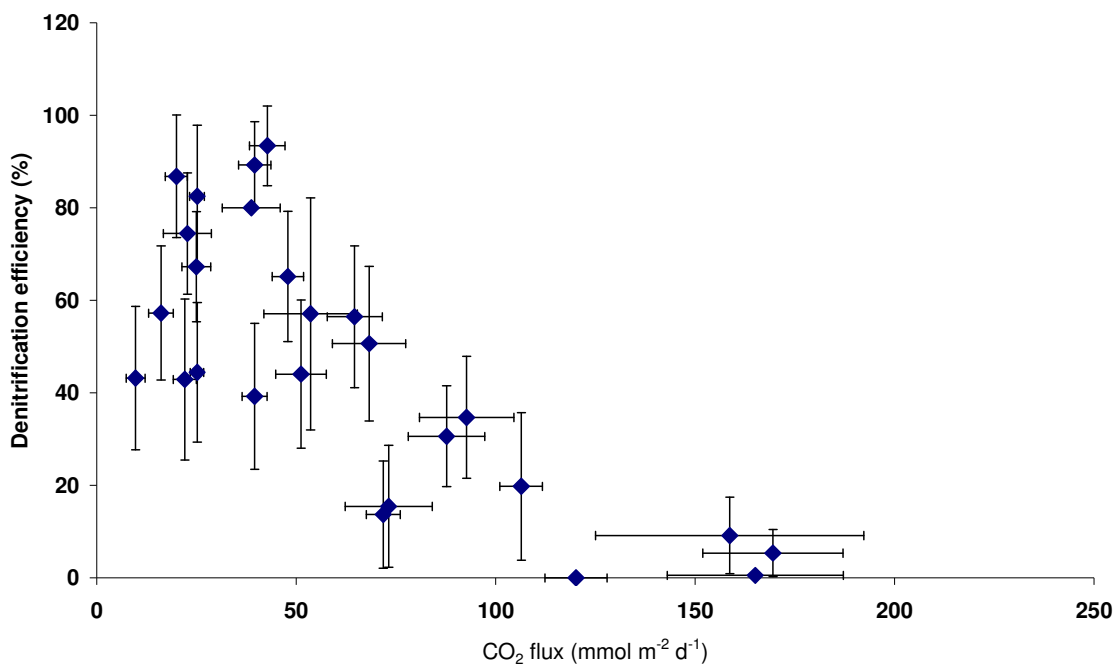


Figure 10 Variation of denitrification efficiency with carbon supply in deep sites

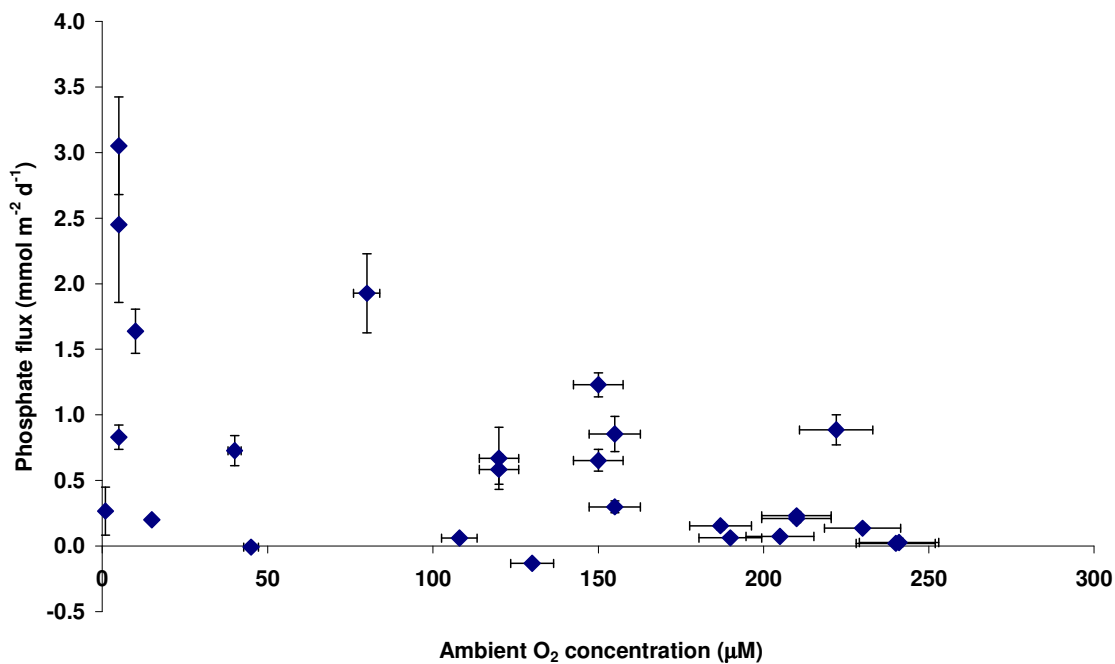


Figure 11 Variation of phosphate flux with ambient oxygen concentration in deep sites

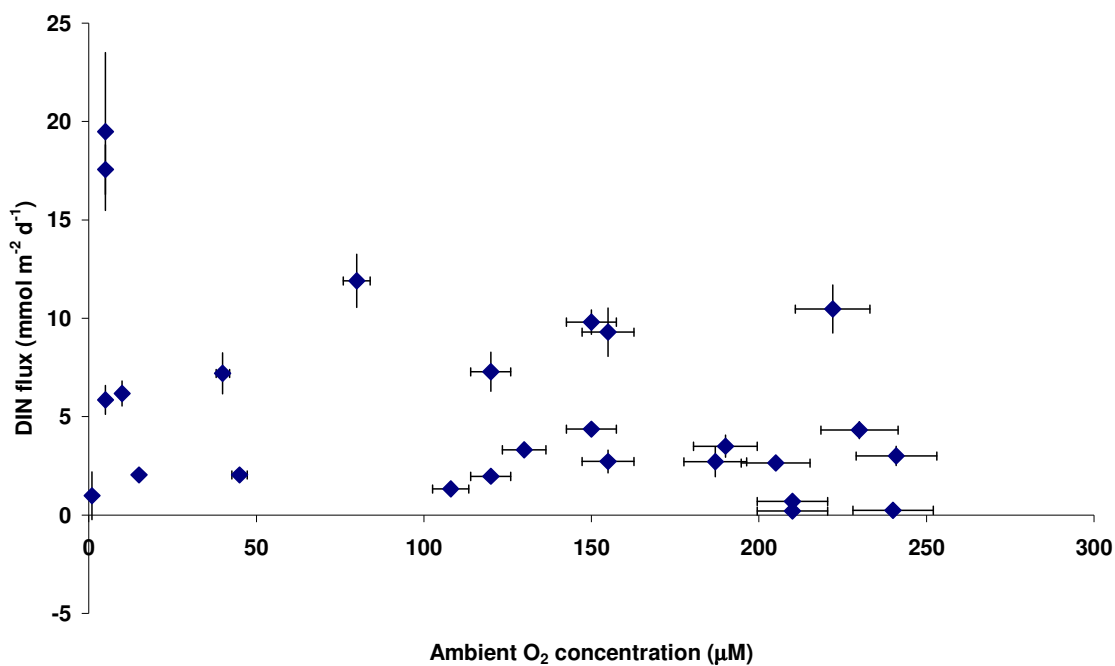


Figure 12 Variation of DIN flux with ambient oxygen concentration in deep sites

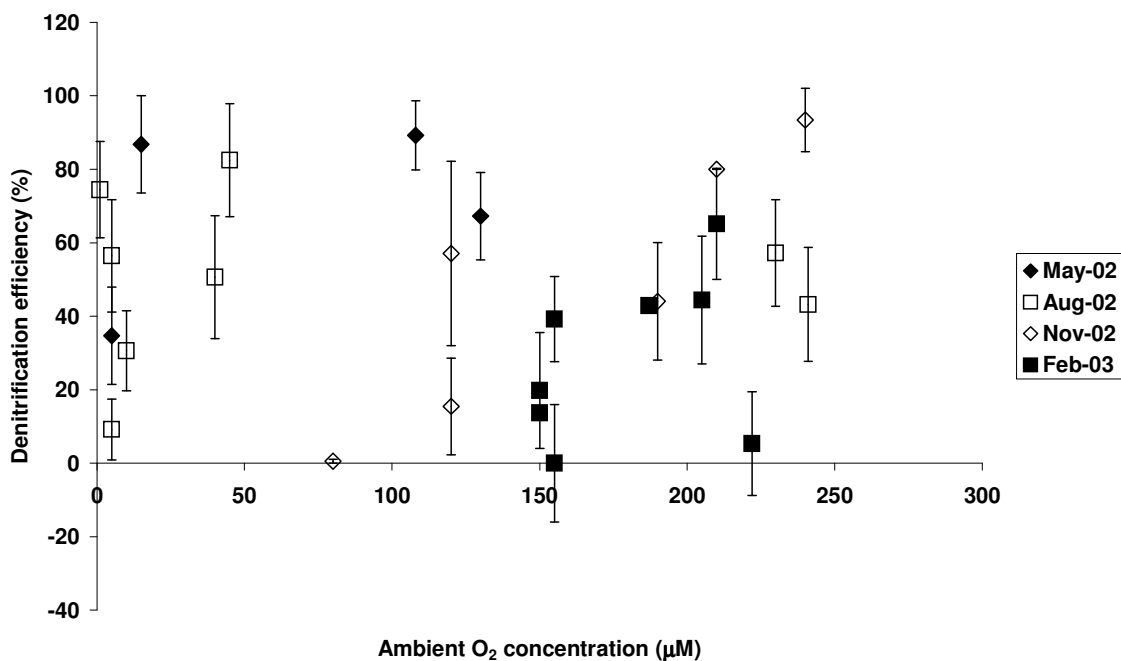


Figure 13 Variation of denitrification efficiency with ambient oxygen concentration in deep sites

Both high carbon dioxide flux and low ambient dissolved oxygen concentrations work in the same direction, enhancing phosphate flux. On the other hand, the stronger relationships of DIN flux and

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denitrification efficiency with carbon supply than with ambient oxygen concentrations suggest that conditions in the near-surface sediments are more important for nitrification/denitrification than are those in the overlying water.

4.5 Implications for CSIRO model calibration

The CSIRO biogeochemical model for the Gippsland Lakes (Parslow *et al.* 2001) was based on the CSIRO PPBES model (Murray and Parslow 1996), with several significant enhancements. These included:

- inclusion of microphytobenthos;
- new formulations for plant growth in response to light and nutrients;
- modelling of stratified water column; and
- improved modelling of sedimentary processes.

In particular, the revised model added dissolved oxygen concentration to carbon supply as a controlling factor on nitrification, denitrification and phosphorus exchange. This was based on an expectation that nutrient fluxes depend on the supply of organic matter to the bottom, and that the recycling processes in the sediment may be modified under anoxic conditions in a stratified water column.

Longmore *et al.* (2001) found that deep-water phosphate fluxes in the Gippsland Lakes correlated better with dissolved bottom-water oxygen concentration than carbon oxidation rate. In the present study, the opposite was found. This may not be a problem for the model, since it includes both factors, and they co-vary. Those parts of the modelling of *Nodularia* growth based on the phosphate flux may be valid.

In contrast, CSIRO acknowledged (Parslow *et al.* 2001) that the model had difficulty reproducing bottom water ammonium concentrations correctly, and badly under-estimated bottom-water ammonium concentrations in Lake Victoria. We propose that this is because the model relies too strongly on dissolved oxygen concentrations to limit denitrification. We have found no relationship (at least in deep water) between denitrification efficiency and dissolved oxygen concentration, with high efficiency possible at low bottom-water dissolved oxygen concentrations (Fig 10). Such observations run counter to our current understanding of the denitrification process, unless the nitrate being denitrified comes from the water column, rather than from the oxidation of ammonium in the sediment. This could only have been true for the May 2002 incubations, where the highest ambient nitrate concentrations (about 1 μM) coincided with highest N_2 fluxes. For all other incubations, ambient nitrate concentrations were close to zero, and the water column could not have been the source of nitrate for denitrifying microbes. A family of bacteria has recently been identified in the anoxic Black Sea and in sediments that oxidise ammonium to N_2 under anaerobic conditions (called the anammox process; Kuypers *et al.* 2003), using nitrite as the oxygen source. Such a process could lead to the observation of high denitrification with an anoxic water column, though a supply of nitrite would still have to be found. If the anammox process is important in Gippsland Lakes sediments, the CSIRO model would require modification. We have shown in the current work that there is a strong relationship between DIN flux and carbon flux, and denitrification efficiency and carbon supply. It may be that the CSIRO model would reproduce observations more closely if the dependence within the model of N processes on ambient oxygen concentration was removed.

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We have shown above that there are significant differences in benthic nutrient fluxes between deep and shallow waters in the Gippsland Lakes. We still don't know where the division between shallow and deep occurs, and all this implies for total flux estimates. It is not yet clear what governs the differences, which do not appear to have been taken into account in the CSIRO model. Overall fluxes in the Gippsland Lakes are dominated by those from the deeper waters, and incorporating shallow-water processes into the existing model based on deep water fluxes would be an enhancement, rather than a fundamental change.

The CSIRO model predicts low algal biomass in dry years, suggesting that catchment inputs are the key driver of blooms. Simple calculations here indicate that benthic fluxes could provide enough nutrients, even in a dry year, to drive a large bloom. If these are both true, it suggests that *Nodularia* blooms depend on a catchment input other than nutrient (e.g. a fall in salinity, trace growth factor) to trigger a bloom. If so, nutrient reductions from the catchment may not reduce algal bloom size or frequency. More research is required into bloom triggers (one study has just been completed, and another about to commence).

5 Acknowledgments

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Appendix 1. Estimates of nutrient requirements for an algal bloom

Assumptions:

1. Benthic flux of $5 \text{ mmol N m}^{-2} \text{ d}^{-1}$ and $1 \text{ mmol P m}^{-2} \text{ d}^{-1}$ applies over 40 km^2 of lake area.
2. Algal bloom of $100 \text{ mg chlorophyll } a \text{ m}^{-3}$ occurs over 100 km^2 of lake surface in a layer 1 m deep, and builds up over 10 days.
3. Conversion from chlorophyll to N is:

$1 \text{ mg chlorophyll} = 25 \text{ mg C}$; $\text{C:N} = 5.7 \text{ (w/w)}$ and $\text{N:P} = 16 \text{ (mol/mol)}$;
hence $1 \text{ mg chlorophyll} = 0.31 \text{ mmol N} = 0.019 \text{ mmol P}$.

Over 40 km^2 , benthic fluxes are $5 \times 40 \times 10^6 \text{ mmol N d}^{-1}$ and $40 \times 10^6 \text{ mmol P d}^{-1}$.

Over 10 days, benthic fluxes may provide $2 \times 10^9 \text{ mmol N}$ and $4 \times 10^8 \text{ mmol P}$.

Chlorophyll content of bloom is $100 \text{ mg chlorophyll m}^{-3} \times 100 \times 10^6 \text{ m}^2 \times 1 \text{ m}$
 $= 1 \times 10^{10} \text{ mg chlorophyll}$.

Nutrient requirement of bloom is $1 \times 10^{10} \times 0.31 \text{ mmol N} = 3 \times 10^9 \text{ mmol N}$ and $2 \times 10^8 \text{ mmol P}$.

Benthic fluxes can therefore supply $(2 \times 10^9)/(3 \times 10^9) = 67\%$ of N requirement and

$$(4 \times 10^8)/(2 \times 10^8) = 200\% \text{ of P requirement.}$$

Under these assumptions, benthic fluxes from the deeper sediments could provide most of the N, and all of the P, required for a substantial algal bloom in the Gippsland Lakes. These assumptions are probably conservative. For example, the area-weighted average inorganic N flux from Table 3 is $1.77 \text{ mmol m}^{-2} \text{ d}^{-1}$, but applies over 341 km^2 of lake area, and amounts to three times the total flux used here.