

Chapter 8

Nutrient Cycling in Lake Malawi/Nyasa

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Introduction

A primary objective of limnological research within the SADC/GEF project is to understand how nutrients control algal dynamics (and ultimately fish community dynamics) in Lake Malawi/Nyasa, and to be able to predict the consequences of changes in the nutrient cycles. The need for such a predictive ability is real. Changes that have occurred in the Laurentian Great Lakes (Ragotzkie 1988), in the Baltic Sea (Larsson et al. 1985; Hansson and Rudstam 1990) and in Lake Victoria (Hecky 1993; Bootsma and Hecky 1993) underline the strong links between nutrient dynamics, algal ecology and fish ecology, and indicate that large size does not make the African Great Lakes immune to human activities in their watersheds. While the population density within the Lake Malawi/Nyasa watershed is not as high as that around Lake Victoria (Chapter 1, Fig. 1.3), with continued population growth it is inevitable that land use patterns will change around the lake, and these changes will almost definitely be accompanied by changes in nutrient input to the lake. Because changes in nutrient input will have implications for algal and fish ecology, an understanding of how nutrients enter the lake and how these nutrients are cycled once they are in the lake is essential in the development of a whole-lake management plan. Only such an understanding will allow us to predict the impact of changes in nutrient input to the lake, and determine the best course of action to prevent or mitigate undesirable changes.

The hydrology of the lake underscores the need for an understanding of the lake's nutrient cycle. Due to thermal stratification, the lake is divided into three main water layers, an upper layer (the epilimnion), a middle layer (the metalimnion), and a bottom layer (the hypolimnion). Based on measurements of chlorofluorocarbon-12, which is useful as a tracer of vertical mixing (see Chapter 4), the boundaries between these layers are at approximately 105 m and 220 m. If rivers carry a large proportion of nutrients into the lake, and if these nutrients are mixed throughout the entire volume of the lake, then an increase in river nutrient concentration will not immediately result in a significant nutrient concentration within the lake, due to dilution by the lake's large volume (see Fig. 1.2 in chapter 1). In this case, monitoring nutrient concentrations within the lake is not a sensitive method of determining whether nutrient inputs to the lake are changing. Knowing the major nutrient sources, and monitoring these sources, would allow changes to be detected at an earlier stage. However, if river nutrients are retained within the epilimnion, and if horizontal advection is slow relative to the time scale of river inputs, then increased river nutrient concentrations can have a localized, immediate influence on plankton dynamics within surface waters. In this case, the lake's great volume does not serve as a protective buffer.

Figure 8.1 illustrates the various components of a generalized nutrient cycle in a lake. The nutrient cycle can be divided into three broad categories:

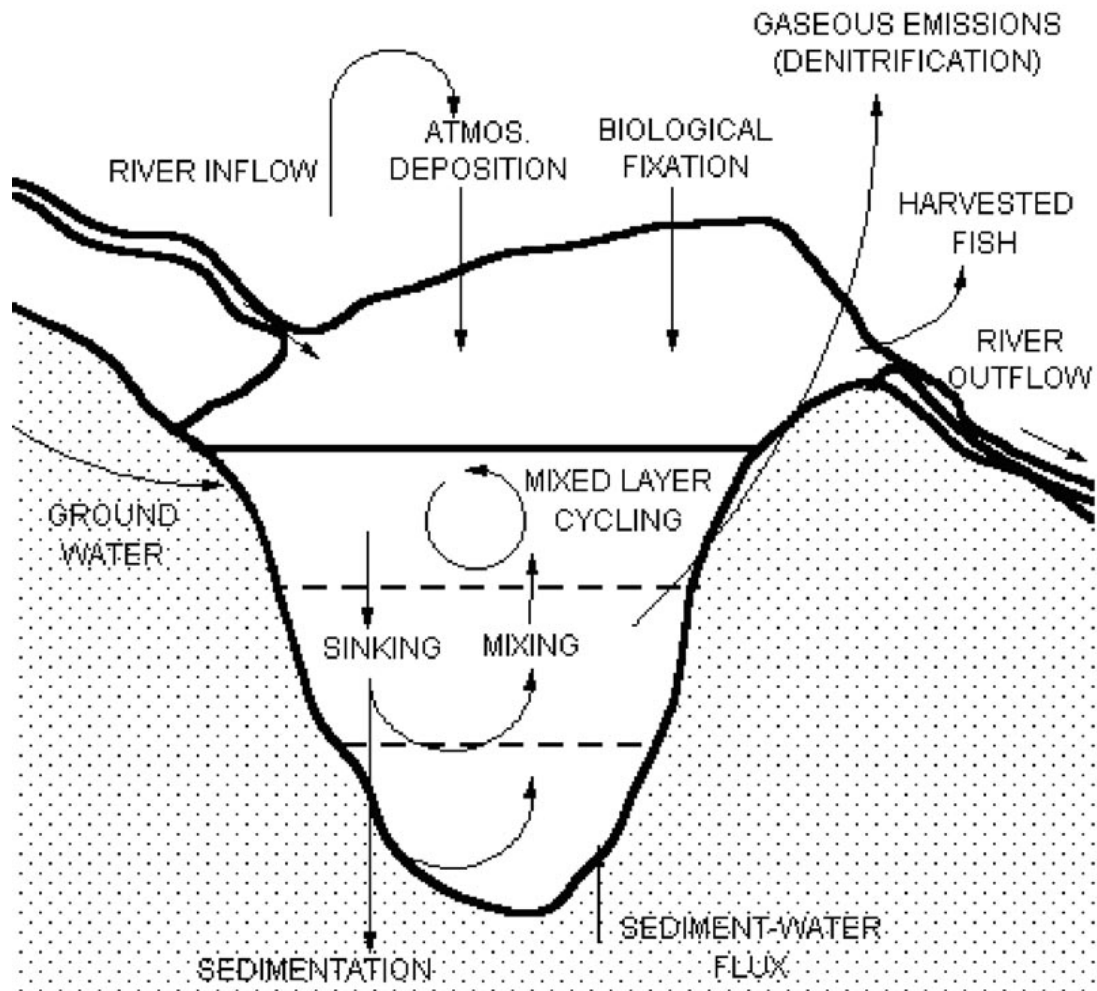


Figure 8.1. Illustration of a generalized, simplified nutrient cycle in a lake.

1. Nutrient inputs (rivers, atmospheric deposition, groundwater, and biological fixation in the case of carbon and nitrogen).
2. Internal nutrient cycling (cycling within each depth layer, sinking of particulate matter, exchange of dissolved nutrients between layers, and cycling between the sediments and overlying water).
3. Nutrient outputs (rivers, sedimentation, gaseous emissions, and fish harvesting).

Internal nutrient cycling is of interest because it determines the distribution of nutrients within the system. From the perspective of algae and fish, nutrient supply to the euphotic zone (the upper layer of water in which there is sufficient light to support photosynthesis) is of greater relevance than the supply to the lake as a whole, because it is within the euphotic zone that nutrients can be used for algal production. Therefore, we have attempted to construct a nutrient budget both for the lake as a whole, and also for the epilimnion (in which the euphotic zone is situated).

The nutrients of primary concern are nitrogen, phosphorus, and silicon. With few exceptions, algal productivity in lakes is controlled by either nitrogen or phosphorus (Hecky and Kilham 1988; Hecky et al. 1993). Silicon does not control productivity of the algal community as a whole, but it is essential for diatoms, which are often an important food source for zooplankton and fish.

Of the 12 nutrient pathways shown in Fig. 8.1, direct measurements are available for the following:

1. River input (chapter 2)
2. River output (chapter 2)
3. Atmospheric deposition (chapter 3)
4. Nitrogen fixation (chapter 6)
5. Particulate sinking rates (chapter 7)
6. Sediment burial (chapter 7)
7. Vertical exchange of dissolved nutrients (reported below)

The following were not measured directly:

1. Groundwater flux
2. Internal nutrient cycling within layers
3. Nutrient flux from sediments to overlying water
4. Gaseous emissions (e.g. denitrification)
5. Fish harvesting

While groundwater may have high nutrient concentrations, the amount of water entering the lake as groundwater is probably very small relative to the amount entering through rivers and as direct precipitation (Owen et al. 1990), and therefore groundwater can probably be safely ignored as a nutrient source for the lake as a whole.

Internal cycling of nutrients within the epilimnion may have important implications for plankton productivity and composition within surface waters (see chapter 6 for more information on the relationship between plankton and nutrient dynamics), and it undoubtedly increases the retention time of nutrients within the epilimnion. However, it does not represent a net nutrient flux for the epilimnion, and therefore does not need to be considered in a whole-lake or epilimnetic nutrient budget.

A significant fraction of the dissolution of particulate nutrients can occur after particulate material has settled to the bottom, resulting in a net positive flux of dissolved nutrients from the sediment to overlying water. In constructing a nutrient budget for the epilimnion, the flux of nutrients from metalimnetic and hypolimnetic sediments can be ignored, since this flux will be accounted for in the measurement of upward nutrient flux from the metalimnion to the epilimnion. Because nutrients regenerated within epilimnetic sediments must have originated as particulate material settling out of the epilimnion, they are not new nutrients *per se*, so ignoring this flux does not affect the epilimnetic nutrient budget. However, a measurement of sediment-water nutrient flux would allow an estimate of

the fraction of settling particulate nutrients that is permanently buried in epilimnetic sediments. In the budget presented here, it is assumed that nutrient burial within epilimnetic sediments is negligible. Although this assumption will result in an underestimate of net nutrient outputs for the epilimnion, this error will be relatively small since only 20% of the epilimnion surface area is underlain by epilimnetic sediment, i.e. most particulate material sinking out of the epilimnion goes directly to the metalimnion.

Gaseous emissions of P and Si can be ignored, since these nutrients have no volatile forms. However, deep vertical profiles of the various dissolved nitrogen species indicate that denitrification (the bacterial conversion of nitrate (NO_3^-) to nitrite (NO_2^-), nitrous oxide (N_2O) and nitrogen gas (N_2)) is occurring within the water column near the oxic-anoxic interface (discussed more fully below). While there are several lines of evidence for the importance of denitrification as a nitrogen loss pathway in Lake Malawi/Nyasa, direct measurements of denitrification in the water column are technically difficult to perform and have not been successfully done. At present, we can only derive a qualitative estimate of this flux.

While fish catch is the nutrient output that is of most direct interest to the people living around the lake, it makes a very small contribution to the whole-lake nutrient budget (although fish production is very much influenced by nutrient dynamics). Based on measurements of fish catches and fish biomass in the lake (Lewis and Tweddle 1990; Menz et al. 1995; Allison et al. 1995; Thompson 1995) a reasonable estimate of the total fish catch for Lake Malawi/Nyasa is 30,000 to 100,000 T per year. When converted to nutrient concentrations, a catch of 100,000 T per year results in N and P losses that are almost equal to the PN and PP losses via river outflow. As demonstrated below, these losses are small relative to other loss pathways, and therefore the exclusion of fish catch from the nutrient budget will not significantly affect the conclusions.

The Flow of Nutrients in Rivers

Previous attempts at constructing a nutrient budget for Lake Malawi/Nyasa (Bootsma and Hecky 1993; Bootsma et al. 1996) have resulted in estimates of river N and P fluxes much lower than those determined in the present study (see Table 2.11, chapter 2). This difference is due almost entirely to the greater particulate N and P fluxes measured recently. Previous estimates were based primarily on river samples that had been collected around April, while the more recent work has shown that the majority of river nutrient flux occurs in the early part of the rainy season, during December and January.

Because a large portion of nutrients entering the lake via rivers is in particulate form, it is important that the fate of particulates is considered when constructing a nutrient budget for the whole lake and for the epilimnion. Specifically, information is needed on where particulate nutrients go once they have entered the lake. Are they deposited near shore or do they flow to the pelagic zone? Are they retained in the epilimnion, or do they sink to deeper water? In addition, the availability of these nutrients needs to be assessed. If they remain in particulate form, they may not be immediately available for cycling within the lake, whereas if they are soluble they will be made available for uptake by bacteria and algae.

Particulate phosphorus is present in numerous forms, including organic P originating from organisms, mineral P such as hydroxyapatite, ferric phosphate and minerals such as ferric hydroxides, clays and calcium carbonate which adsorb P, and P adsorbed on to detrital seston (dead particulate organic material). The availability of this particulate phosphorus for biological processes depends on a number of factors, including solubility, dissolved P concentration, metal concentrations (especially iron), and redox potential, which is controlled to a large degree by dissolved oxygen distribution. As indicated in chapter 2, measurements of the various fractions of particulate P in river samples indicate that a relatively small percentage is in a "bio-available" form, i.e. a form that is relatively soluble and available for biological uptake. However, even less soluble forms may eventually become available through slow dissolution, particularly if these forms encounter an anoxic environment.

The whole-lake nutrient budget presented below uses measurements of total particulate phosphorus fluxes for all inputs and outputs. While this treatment results in the loss of some biologically relevant information, it is the only approach that can be taken at present in an attempt to produce a balanced budget (in which total inputs equal total outputs). Our knowledge of phosphorus

dissolution dynamics within the lake is currently insufficient to allow a more detailed analysis of the fate of riverine phosphorus fluxes.

As for the whole-lake budget, the epilimnion nutrient budget deals only with total phosphorus inputs and outputs. The main uncertainty in the epilimnetic phosphorus budget is the exchange of P between sediments and overlying water. Turbulence and bioturbation will result in resuspension of epilimnetic sediments, which will reduce burial rates. However, if a large portion of particulate P in rivers is in the form of large, dense particles, much of this may sink and be buried close to river mouths (see Annex to Chapter 2). In addition, iron and manganese precipitation at the sediment-water interface (Owen et al. 1996) may also result in scavenging of dissolved phosphorus from epilimnetic waters. In the present budget, we assume that the epilimnetic phosphorus burial rate is equal to the sinking flux of particulate phosphorus, as measured in sediment traps.

Unlike phosphorus, particulate nitrogen is rarely in mineral form. Particulate nitrogen in rivers is composed primarily of organisms (living and dead) and dissolved organic and inorganic compounds adsorbed on to particulates. Clays in particular can be effective adsorbers of the ammonium cation (NH_4^+). The adsorption-desorption process is controlled by pH, redox conditions, and the major ion composition of water. Without detailed information on any of these processes, we have relied on measurements of total nitrogen inputs and outputs to construct the whole-lake and epilimnetic nitrogen budgets.

Much of the particulate silicon in rivers is in mineral form, which is not readily available for use by algae in the lake. The particulate silicon data for rivers presented in chapter 2 represents the amount of particulate silicon that is relatively soluble ("available" particulate Si), determined by digesting filter samples in a weak alkaline solution for a fixed length of time. Particulate Si sedimentation rates were determined by analyzing sediment trap samples in the same way. In contrast, Si burial rates are based on the measurement of biogenic Si in sediment cores. In the following budget we use both of these measurements, with the understanding that available particulate Si may be greater than biogenic Si.

While the depth to which riverine nutrients flow after entering the lake is not relevant to the whole-lake nutrient budget, it can have profound effects on the epilimnetic budget. If flow is directly into the epilimnion, then the plankton and fish communities may respond very rapidly to changes in river nutrient fluxes. However, if the flow is to depths greater than 100 m, then temporal fluctuations of nutrient concentrations in the lake's surface waters will be muted relative to those in the rivers, and deep-water processes, such as burial, phosphorus precipitation and denitrification, will prevent a certain fraction of river-borne nutrients from ever being made available to the epilimnion.

The comparison of river water density and lake water density in chapter 2 (Table 2.20) indicates that river water is generally denser than lake surface water, sinking to some depth between the surface and greater than 100 m. This is supported by detailed sediment plume studies near the mouth of the Linthipe River (see annex to chapter 2). CTD profiles collected during the rainy season reveal that these sub-surface plumes can extend far out into the lake (Fig. 8.2). For example, the mid-water turbidity layer observed at Station 900 on January 20 was observed at several other points sampled between Station 900 and Senga Bay, suggesting that this turbidity layer originated from the Linthipe River, which enters the lake approximately 50 km southwest of Station 900 (there are no major tributaries on the east side of the lake in this region).

In order to determine the fraction of river-borne nutrients that enters the epilimnion and the fraction that sinks below the epilimnion, for each river the percentage of river flow that is estimated to descend to below 100 m (chapter 2, table 2.20) was weighted according to total annual suspended solids discharge. The weighted mean for all measured rivers was then determined. This is justified on the basis that a large proportion of river nutrients is in the particulate form, and particulate nutrients were generally correlated to total suspended solids (see chapter 2). The resultant estimate is that 39% of river-borne nutrients is carried directly to depths of greater than 100 m. Based on this estimate and the estimates of river nutrient fluxes, the annual riverine nutrient fluxes to the epilimnion and to deeper waters were derived (Table 8.1).

Table 8.1. Annual riverine nutrient flux to surface (<100 m) and deep (>100 m) waters, based on measured river nutrient concentrations, river discharge, and comparisons of river and lake water densities. Units are $\text{mmol m}^{-2} \text{yr}^{-1}$, normalized to lake surface area. $\text{DIN} = \text{NO}_3^- + \text{NH}_4^+$.

	DIN	TDN	PN	SRP	TDP	PP	SRSi	PSi
< 100 m	2.9-5.1	10.5-17.1	77-182	0.3-0.59	0.61-0.85	4.5-7.0	163-199	232-479
>100 m	1.9-3.3	6.7-11.0	49-117	0.19-0.37	0.39-0.55	2.9-4.5	105-128	148-306

Atmospheric Deposition of Nutrients

The results of atmospheric deposition measurements are presented in chapter 3. Unlike river nutrient measurements, atmospheric deposition measurements are not extensive in space. However, for the main collection site (Senga Bay), there was a high frequency of sampling. Dry deposition was measured every 13 days, and almost all rain events were sampled. The main uncertainty in applying the Senga Bay measurements to the entire lake concerns spatial variability. As discussed in chapter 3 (Fig. 3.9), atmospheric nutrient deposition tends to be greater at stations that are further inland from the lake. Although the Senga Bay collection site usually receives winds that have travelled across the lake, the site is probably still affected to some degree by local terrestrial events, and may therefore experience nutrient deposition rates that are greater than those in the middle of the lake. However, because the site is on the leeward side of the lake, deposition rates may be lower than on the east side of the lake, which experiences winds coming directly off of the Malawi, Mozambique and Tanzania mainlands.

For the purposes of the present budget, we apply the deposition rates measured at Senga Bay, without attempting any correction for spatial variability. Although rain chemistry (and probably dry deposition also) varies greatly between different regions of Africa (Bootsma et al. 1996), the similarity between nutrient deposition rates measured at Senga Bay and Kyela (nearly 500 km apart) provides reassurance that the Senga Bay deposition rates are applicable to the entire lake.

Apart from spatial variability, temporal variability of atmospheric nutrient deposition is also of concern. The nutrient budget presented below reports nutrient fluxes on an annual basis, using atmospheric deposition data from May 1997 to April 1998, which corresponds approximately to the period used to estimate river nutrient fluxes. Some individual compounds exhibited significantly different atmospheric deposition rates between the 1996/97 and 1997/98 rainy seasons (chapter 3, table 3.3). However, total nitrogen deposition rates differed by only 5% between the two years, while total phosphorus deposition rates differed by 27 %. While there is still some uncertainty about inter-annual variation and long term absolute deposition rates, the measurements made at Senga Bay are adequate to allow an assessment of the relative importance of atmospheric deposition to the lake's nutrient budget.

Nitrogen Fixation

Nitrogen fixation, the conversion of N_2 gas to organic N, is carried out by cyanobacteria (blue-green algae) in aquatic ecosystems. In general, it is only the heterocystous forms of cyanobacteria that fix nitrogen, since the fixation process only occurs in the anoxic environment that is maintained within thick-walled heterocysts. While nitrogen-fixing cyanobacteria have always been present in Lake Malawi/Nyasa (Beauchamp 1953; Jackson et al. 1963; Hecky and Kling 1987; Bootsma 1993), they have never been a persistent, dominant component of the phytoplankton community. However, there

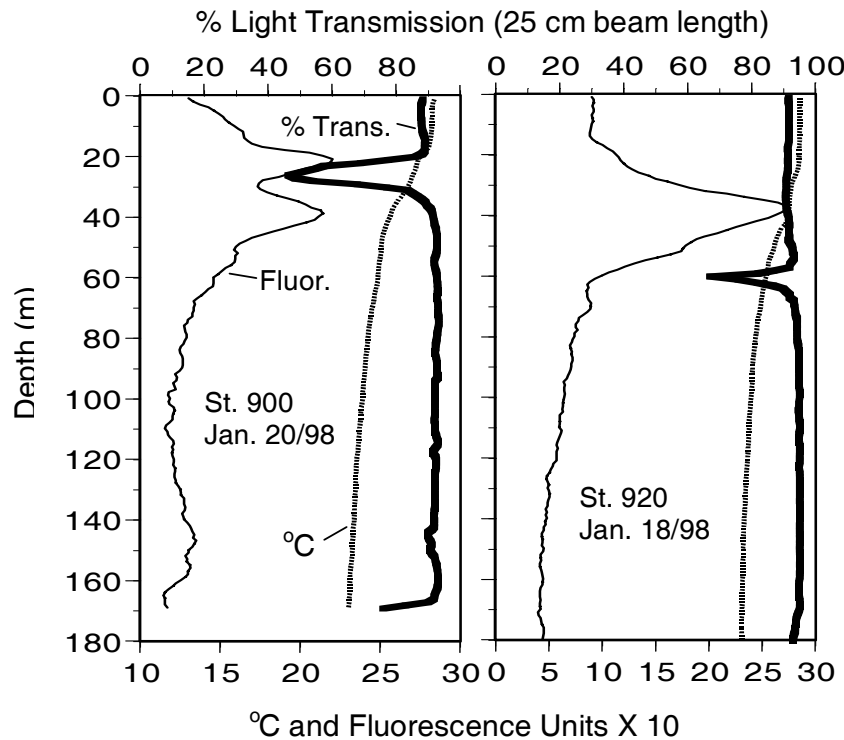


Figure 8.2. Profiles of water clarity, temperature, and algal fluorescence measured at two pelagic stations in January 1998. See figure 1.4 in chapter 1 for station locations.

is evidence that they are becoming more pervasive in the form of *Anabaena* and *Cylindrospermopsis* blooms (see chapter 7).

While the dominance of the pelagic phytoplankton community by nitrogen fixing cyanobacteria is seasonal, within the benthic (bottom) algal community heterocystous cyanobacteria are always present and often dominant, particularly in rocky zones. The most common genera are *Calothrix* and *Rivularia*.

Measurements have been made of both pelagic (chapter 6) and benthic (S. Higgins, unpubl.) nitrogen fixation rates, allowing some assessment of the importance of this process as a potential nitrogen source for the lake. S. Higgins has measured mean epilithic (rock surface) nitrogen fixation rates of 125, 71.4 and 14.3 $\text{mmol N m}^{-2} \text{h}^{-1}$ at depths of 2, 5 and 10 m respectively. If the intermediate rate of 71.4 $\text{mmol N m}^{-2} \text{h}^{-1}$ is applied to the entire rocky littoral zone, then an approximate daily N fixation rate of 714 $\text{mmol N m}^{-2} \text{d}^{-1}$ is derived by multiplying the hourly rate by 10. In order to extrapolate this rate to the entire lake, an estimate of the area of rocky littoral zone in the lake is required. Ribbink et al. (1983) estimated that approximately 30% of the lake's shoreline is rocky. Assuming that the average bottom slope of the rocky littoral zone is 30°, and that N-fixation is negligible below 10 m (due to low irradiance), and that the lake's perimeter is 1500 km, the surface area of rocky, littoral N-fixation zone within the lake is estimated to be 9.0 km^2 . (Note that this does not account for bottom roughness, which will increase surface area.) Applying the N fixation rate of 714 $\text{mmol N m}^{-2} \text{d}^{-1}$, multiplying by 365 days per year, and normalizing to the lake's entire surface area, an annual nitrogen fixation N flux to the whole lake of 78 $\text{mmol m}^{-2} \text{yr}^{-1}$ is calculated. The actual total benthic fixation rate may be much greater, since we have not accounted for possible fixation in the shallow sediments.

Pelagic nitrogen fixation rates have been measured on two occasions, once in November of 1996 and once in November-December 1997 (see annex to chapter 6). This is typically the time of year when heterocystous cyanobacteria are abundant (Hecky and Kling 1897). Patterson and Kachinjika (1995) found the frequency of heterocysts on *Anabaena* filaments to be greatest at this time of year, but this does not appear to be the case in all years (Bootsma 1993). Offshore rates measured in 1996 were between 0.0022 and 0.0027 $\mu\text{mol N L}^{-1} \text{h}^{-1}$ near the surface, and gradually decline to near-zero rates at 80 m. Rates measured over a 13-day period offshore from the Senga Bay lab varied greatly from day to day, from undetectable to nearly 0.03 $\mu\text{mol N L}^{-1} \text{h}^{-1}$.

Due to the small number of dates and locations for which pelagic N fixation was measured, and the high variability between dates, little can be said about its spatial and temporal variability, and an accurate estimate of annual N fixation for the entire lake is not possible at this time. If a rate of 0.001 $\text{mmol N L}^{-1} \text{h}^{-1}$ is taken as representative of the entire euphotic water column during the November 1996 study period, and this rate is multiplied by a 60 m euphotic zone depth (Degnbol and Mapila 1982; Bootsma 1993) and by 10 hours per day, it is equivalent to a whole-lake annual N-fixation flux of 219 $\text{mmol N m}^{-2} \text{yr}^{-1}$. However, the results of the 1997 experiments indicate that the error of this estimate may be an order of magnitude in either direction. The potential significance of N-fixation to the whole-lake nitrogen budget is further discussed below.

Sinking and Burial of Particulate Nutrients

Because the flux of nutrients out of the lake via the Shire River is much lower than the nutrient flux into the lake, there must be a major loss mechanism within the lake in order for total nutrient losses to equal total inputs. Apart from denitrification, which is an important nitrogen loss pathway, the sinking and burial of particulate nutrients is the major mechanism by which nutrients are lost from the lake. With regard to the whole-lake budget, only sediment burial is of interest, and this flux is estimated based on sediment core analysis. But for the epilimnetic budget, measurements of particulate nutrient sinking rates out of the epilimnion are required; these measurements were made using sediment traps moored at two locations in the lake.

Estimates of sinking and burial rates are reported in chapter 7. Sinking rates most applicable to the epilimnion are those measured in sediment traps fixed at 100 m. Rates measured at this depth at the two mooring stations are given in table 8.2. Total annual particulate C and N sedimentation rates were similar at the two stations, while particulate P and Si sedimentation rates were greater in the south than near the centre of the lake. Rather than discount this spatial variability by calculating a

Table 8.2. Particulate nutrient sedimentation rates measured in 100 m sediment traps moored at Station THRM2 and Station 917. Units are $\text{mmol m}^{-2} \text{day}^{-1}$, except for annual rates, which are $\text{mmol m}^{-2} \text{yr}^{-1}$. Particulate Si samples marked * were not measured directly, but were calculated using an observed particulate Si : total particulate ratio of $0.00465 \pm 0.0019 \text{ mmol mg}^{-1}$.

Period	Station	C	N	P	Si
May 14 – Sep. 8/97	THRM2	1.85	0.18	0.014	1.94
Sep. 8 – Dec. 15/97	THRM2	3.07	0.25	0.030	3.30
Dec. 15 – May 8/98	THRM2	6.62	0.66	0.038	3.89*
Annual Sedimentation	THRM2	1496	143	10.2	1129
May 15 – Sep. 14/97	917	2.08	0.18	0.012	1.24*
Sep. 14 – Dec. 16/97	917	4.84	0.47	0.022	2.10
Dec. 16 – May 7/98	917	5.13	0.57	0.026	1.94*
Annual Sedimentation	917	1464	150	7.4	636

mean sedimentation rate, sedimentation rates from both stations were used as “high” and “low” values in the epilimnetic nutrient budget.

Pre-1960 particulate nutrient burial rates were remarkably similar at the two stations for which sediment grabs were analyzed (chapter 7, table 7.2). However, there was a large temporal change in burial rates of P and Si at the southernmost grab site, with burial rates being much higher after 1960 (see Figs. 7.7 and 7.8 in chapter 7). Mean pre-1960 burial rates have been used as a “low” estimate in the budget, and the mean of south (grab SB3) and north (grab SB2) post-1960 burial rates have been used as a “high” estimate.

Only particulate P and Si analyses have been done on deep grab samples, and therefore we have no direct measurement of nitrogen burial rates. For the nutrient budget, an approximate rate was determined by multiplying the measured P burial rates by the mean molar N:P ratio measured in deep sediment traps. This ignores any differential recycling of N and P that may occur in the profundal sediments, but is sufficient to provide a first approximation of the N burial rate.

A further potential source of error in the burial rate stems from the uncertainty about the degree of sediment focusing in the lake. Re-suspension and lateral transport of sediments in lakes results in the gradual movement of shallow sediments to deeper depths, which can result in overestimates of sedimentation and burial rates in deeper parts of the lake, and underestimates in shallower parts. That this is likely a significant process in Lake Malawi/Nyasa is attested to by the observation that, at Station THRM2, total particulate sedimentation rates in the deepest trap (180 m) were always greater than the rates measured in the 100 m trap (Table 8.3). Not surprisingly, the greatest proportional difference between the 100 m and 180 m traps was recorded in the May to September collection period. This is when the persistent, strong southeast winds blow, and water turbulence and sediment re-suspension can be expected to be greatest.

At present it is impossible to assess how the burial rates estimated from grab samples may be affected by sediment focusing. We therefore present the data as described above, with the caveat that there is potential overestimate due to focusing.

Table 8.3. Particulate sedimentation rates ($\text{mg m}^{-2} \text{ day}^{-1}$) measured at three different depths at Station THRM2 (maximum depth at station = 200 m).

Depth (m)	May – Sep. 1997	Sep. – Dec. 1997	Dec. – May 1998
100	384	520	836
140	630	717	959
180	2697	1483	1238

The Flux of Dissolved Nutrients from Deep Water to the Epilimnion

Lake Malawi/Nyasa is meromictic, i.e. it never undergoes complete vertical mixing. As a result of this permanent stratification, the decomposition of particulate material in the deep waters of the lake results in a loss of dissolved oxygen and an accumulation of dissolved nutrients in the metalimnion and hypolimnion (Fig. 8.3). Periodic exchanges of this nutrient-rich deep water with epilimnetic water can have a dramatic influence on the chemistry and plankton and fish ecology within the epilimnion. Hence this exchange, while not representing a new nutrient flux to the lake, is important to consider within a nutrient budget.

There are several mechanisms by which deep-water nutrients can be introduced to the epilimnion. 1. Upwelling. This is the physical advection of nutrient-rich deep water to shallower depths, resulting

from currents within the lake. These currents can arise due to wind events, horizontal temperature gradients, and horizontal pressure gradients. In exceptional cases, they can also be caused by tectonic activity. 2. Turbulent diffusion. This is a mixing process that occurs at the horizontal boundaries between adjacent water strata, due to differences in velocity between the strata (shear stress). This process also depends on water movement, resulting from the same factors mentioned above. 3. Molecular diffusion. This represents the physical diffusion of a dissolved substance from an area of high concentration to an area of low concentration. It is not accompanied by the physical movement of water. This process is very slow, and compared to the other processes mentioned here, it is negligible. 4. Vertical entrainment. This occurs when a layer of water cools and becomes isothermal (and therefore of the same density) with the layer underneath it. As a result, the two layers can be mixed with minimal kinetic energy. The heating and cooling of lakewater is controlled by short wave radiation, long wave radiation, the difference between water temperature and overlying air temperature, and evaporative cooling, which is a function of wind speed, humidity, and the temperature difference between the lake surface and the overlying air. (In some lakes, the temperature of rain and river water is also an important component of the heat budget, but these factors likely have a negligible effect in Lake Malawi/Nyasa).

It is noteworthy that, apart from molecular diffusion and tectonic activity (both of which are minor factors controlling the movements of water and nutrients in lakes), all of the above processes are controlled by meteorological variables. Hence, it is weather conditions that control the vertical exchange of nutrients within the lake.

An appreciation of the importance of weather in controlling nutrient and plankton dynamics can be gained by examining the lake-wide distribution of temperature, nutrients and chlorophyll *a* (Fig. 8.4). The southeast wind (*mwera*) begins to blow in May, pushing warm surface water to the north. The surface water that is blown out of the south is replaced by cooler water coming up from depth, as shown by the isotherms, which are tilted upward from north to south (fig. 8.4A). A north-south gradient is also evident for chlorophyll *a* concentration, which is more than three times greater at the southern end of the southeast arm than in the more northern pelagic regions (fig. 8.4B). This gradient is probably due to the upward flux of nutrients at the southern end of the lake. Often, a greater dissolved nutrient input to surface waters is not reflected as higher nutrient concentrations, because plankton assimilate the nutrients as fast as they are supplied. In figure 8.4C, there is not much evidence of a horizontal gradient in NO_3^- concentrations. However, the relationship between thermal structure and nutrient dynamics is evident in the higher epilimnetic SRSi concentrations in the southern part of the lake (fig. 8.4D). This is probably due to the fact that not all phytoplankton assimilate silicon, and therefore SRSi serves as a semi-conservative indicator of mixing dynamics.

Direct quantification of any of the vertical exchange processes is technically difficult. However, with information on the vertical profiles of water density and nutrient concentrations, along with meteorological data, it is possible to assess the magnitude of nutrient upwelling through mathematical models. Using this approach, nutrient upwelling estimates on different dates in the southeast arm have been estimated (see figures 5.14 – 5.16 in chapter 5). The ranges of estimated nutrient upwelling rates (using the depth of maximum upwelling for each profile) are given in table 8.4.

Table 8.4. Range of nutrient upwelling rates estimated for three different dates in the southeast arm (based on upwelling profiles shown in figures 5.14 – 5.16 in chapter 5). TDN flux available for one date only. DIN = dissolved inorganic nitrogen ($\text{NO}_3^- + \text{NH}_4^+$). See text for meaning of other acronyms. All fluxes are $\text{mmol m}^{-2} \text{day}^{-1}$.

	DIN	TDN	SRP	TDP	SRSi
Upwelling Flux	0.93 – 24.3	22.9	0.18 – 4.2	0.17 – 1.4	7.8 - 133

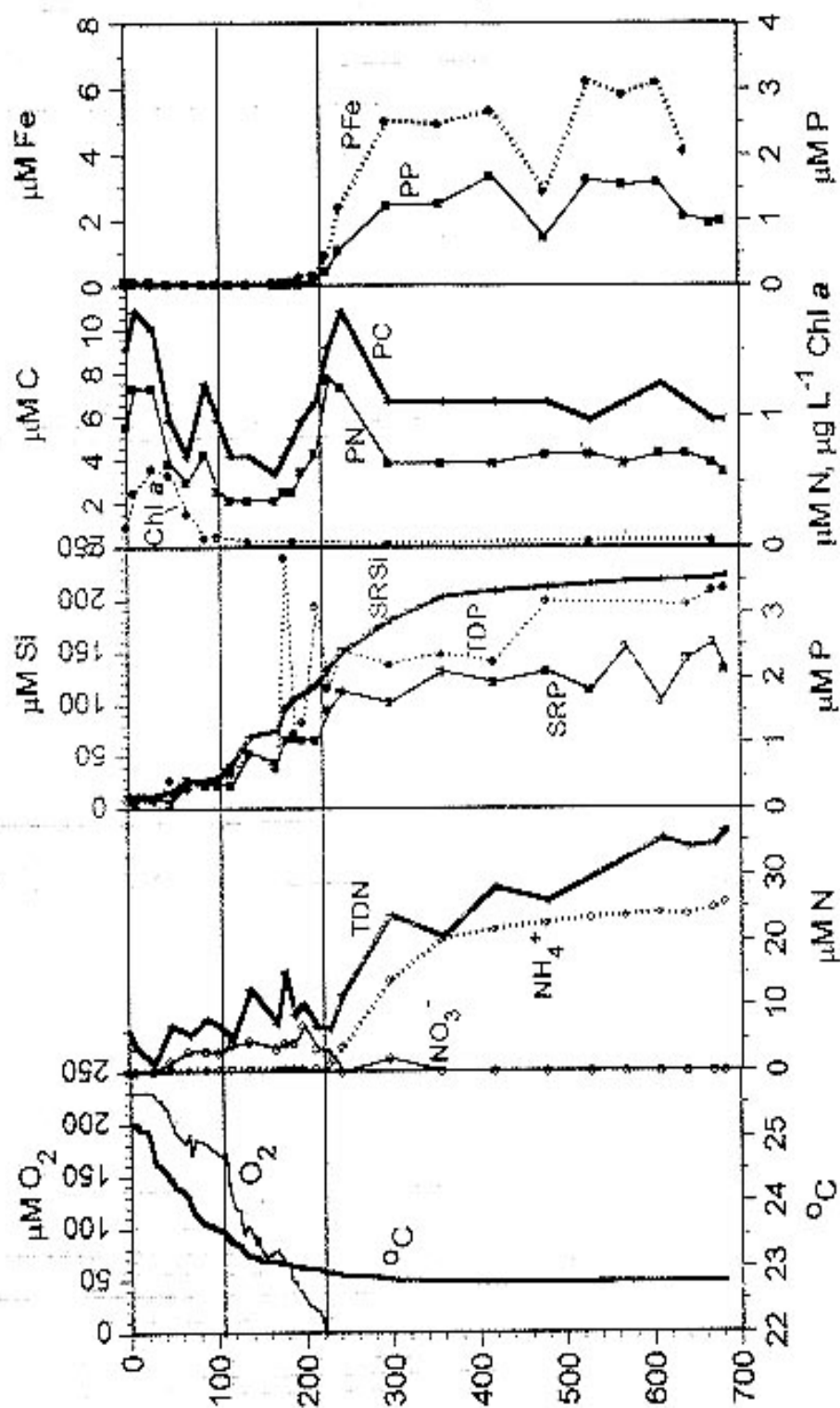


Figure 8.3. Vertical temperature and chemical profiles at station 940, Sep. 13, 1997. Horizontal lines show the boundaries between the epilimnion, metalimnion and hypolimnion, as suggested by the CFC-12 analysis of Vollmer and Weiss (Chapter 4). See text for meaning of acronyms. PFe = particulate iron.

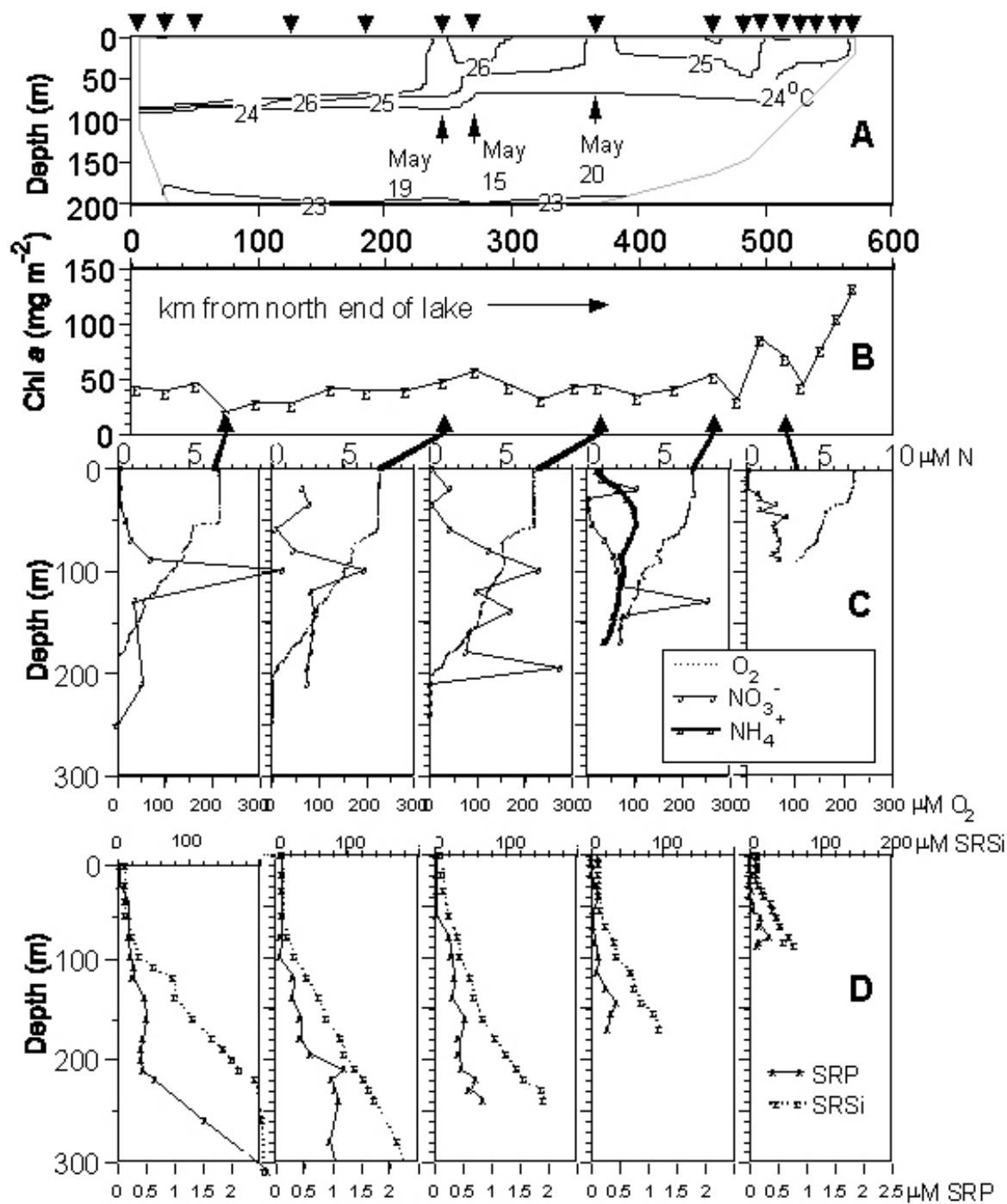


Figure 8.4. Distribution of temperature, chlorophyll *a*, and dissolved nutrients along the lake's north-south axis in May 1997. Chlorophyll *a* values represent the 0-100 m integral.

Upwelling is a local event, and the relative importance of upwelling as a nutrient source to the epilimnion can be expected to vary greatly for different parts of the lake. The upward tilting of isotherms at the south end of the lake, shown in figure 8.4A is a common phenomenon (see chapter 5; Eccles 1974, Bootsma 1993; Patterson and Kachinjika 1995), and upwelling is undoubtedly stronger in the south end of the lake than in most other regions. Therefore, while upwelling is of interest when considering regional plankton dynamics and fish distribution, measuring upwelling in one area does not allow for the total annual nutrient flux to the epilimnion from deeper waters. Not only is upwelling spatially variable, but it represents only one of three major mechanisms by which vertical nutrient flux can occur.

The CFC-12 tracer measurements made by Vollmer and Weiss (chapter 4) permit an estimate of time- and space-integrated vertical exchange between the different layers of water in the lake. While these measurements cannot be used to determine the exact mechanisms by which vertical exchange takes place, they provide an estimate of total water exchange between layers over long periods of time, on the scale of several years.

When combined with data on the nutrient content of the different layers, the long-term vertical exchange rates can be used to estimate vertical nutrient fluxes. The same equations used by Vollmer and Weiss to estimate water exchange rates can be used to estimate nutrient exchange rates. For the epilimnion:

$$\frac{dc_1}{dt} = k_2 \frac{V_2}{V_1} (c_2 - c_1) \quad (1)$$

and for the nutrient flux from the hypolimnion to metalimnion:

$$\frac{dc_2}{dt} = k_3 \frac{V_3}{V_2} (c_3 - c_2) \quad (2)$$

where c_1 , c_2 and c_3 are the epilimnetic volume-weighted nutrient concentrations for the epilimnion, metalimnion, and hypolimnion, k_2 and k_3 are the exchange coefficients for the epilimnion-metalimnion boundary and metalimnion-hypolimnion boundary, and V_1 , V_2 and V_3 are the water volumes of the epilimnion, metalimnion, and hypolimnion. While Vollmer and Weiss measured c (CFC-12 concentrations) and solved the equations for k , nutrient fluxes are derived by applying Vollmer and Weiss's values of k , and solving for dc/dt . Note that equation (2) is slightly different from equation (2) of Vollmer and Weiss (chapter 4), since dc/dt in equation (2) here refers only to the flux from the hypolimnion to metalimnion, and ignores metalimnion-epilimnion exchange.

For each dissolved nutrient, values of c for each layer were determined as volume-weighted means, which represents the concentration of dissolved nutrient in a layer if that layer was homogeneously mixed. Values of c for each layer were determined for each vertical nutrient profile that was sampled:

$$c = \frac{\sum (\Delta Z_i A_i c_i)}{\sum (\Delta Z_i A_i)} \quad (3)$$

where ΔZ_i is the height of the depth interval of a sampled stratum of water, A_i is the total area of the stratum, and c_i is the nutrient concentration measured in the layer i . Values of A_i were determined for each stratum using a third-order polynomial equation describing area as a function of depth:

$$A(\text{km}^2) = 8.929 \cdot 10^{-5} \cdot z^3 - 4.533 \cdot 10^{-2} \cdot z^2 - 52.64 \cdot z + 2.926 \cdot 10^4 \quad \text{where } z = \text{depth in m.}$$

This equation was parameterized using a hypsographic curve derived from the 20 m resolution bathymetric data of Halfman and Johnson (unpubl.) (digitized by P. Cooley). The boundary depth

between the epi- and metalimnion was set at 105 m, while that between the hypo- and metalimnion was 220 m, based on Vollmer and Weiss's interpretation of their CFC-12 profile (chapter 4).

It is obvious from equation (1) that the flux of nutrients from the metalimnion to the epilimnion is a linear function of the difference in nutrient concentration between the two strata. The difficulty in using this equation to estimate annual vertical nutrient flux rates is that the nutrient concentration differences between the epilimnion and metalimnion vary over relatively short periods of time (days to weeks), and vary with location at a given time. The use of a conservative tracer such as CFC-12 results in a k value that integrates time and space. Ideally, each vertical nutrient profile must be matched with a unique k value, since k also varies with space and time.

The best compromise at present is to use the mean nutrient concentrations for each layer, using nutrient profile data from all locations and times. The assumption is that these means are similar to the real time- and space-integrated nutrient concentrations.

The resultant volume-weighted dissolved nutrient concentrations and vertical nutrient fluxes are given in table 8.5. To make all fluxes comparable, the vertical fluxes were normalized to the lake's surface area. Notice that if these rates are divided by 365 to make them comparable to the daily rates in table 8.4, the daily upwelling rates in the southeast arm are much higher than the average daily exchange rate for the entire lake, underlining the importance of upwelling as a local event.

Table 8.5A. Mean volume-weighted dissolved nutrient concentrations for the three water layers (epilimnion, metalimnion, hypolimnion).

Layer	NO ₃ ⁻ (μM)	NH ₄ ⁺ (μM)	TDN (μM)	SRP (μM)	TDP (μM)	SRSi (μM)	Volume (km ³)
Epilimnion	1.95	0.36	6.5	0.19	0.60	19.6	2780
Metalimnion	4.22	0.66	8.1	0.74	1.49	79.0	2330
Hypolimnion	0	18.31	22.6	1.74	2.20	190.0	2718

Table 8.5B. Estimated dissolved nutrient fluxes between water layers (mmol m⁻² yr⁻¹). The three values for TDN, TDP and SRSi represent fluxes based on the minimum, mean and maximum observed differences in volume-weighted nutrient concentrations between strata.

Layer	NO ₃ ⁻	NH ₄ ⁺	TDN	SRP	TDP	SRSi
Meta- to Epilimnion	32.6	4.7	-23.7, 22.6, 96.6	8.1	7.7, 12.8, 22.4	638, 854, 1429
Hypo- to Metalimnion	-20.5	85.7	7.4, 70.3, 109	4.8	0.31, 3.44, 5.78	343, 539, 656

A Nutrient Budget

The estimates of various input and output fluxes, along with assumptions made in estimating the fluxes, are given in table 8.6. Using these fluxes, the sum of N, P and Si inputs and outputs for the whole lake and for the epilimnion were calculated (table 8.7).

Each of the individual nutrient cycles will be discussed separately, followed by a comparison of the budgets of all three nutrients.

Table 8.6. Fluxes of nitrogen, phosphorus and silicon into and out of Lake Malawi/Nyasa (all units $\text{mmol m}^{-2} \text{yr}^{-1}$). The range of river inputs represents the range between minimum and maximum input estimates. River inorganic N fluxes are summed as $\text{NO}_3^- + \text{NH}_4^+$. The range of particulate sinking rates represents the difference between rates measured at Station THRM2 and Station 917 (based on sediment trap collections from 100 m at both stations). The N fixation estimate is based on an N fixation rate of $0.001 \mu\text{mol N L}^{-1} \text{hr}^{-1}$; there is potentially a large degree of error in the annual estimate.

Flux Pathway	NO_3^-	NH_4^+	TDN	PN	SRP	TDP	PP	SRSi	PSi
Rivers to Epilimnion	2.9 – 5.1		10.5–17.1	77-182	0.30-0.59	0.61-0.85	4.5-7.0	163-199	232-479
Rivers to Metalimnion	1.9-3.3		6.7-11.0	49-117	0.19-0.37	0.39-0.55	2.9-4.5	105-128	148-306
River Outflow	0.31		1.71	2.7	0.015	0.033	0.15	3.1	9.8
Atmospheric	33.5	7.2	116	33	0.92	4.2	3.65	35	15.6
N-fixation, pelagic				219					
N-fixation, epilithic				78+					
Vertical 1	32.6	4.7	-24 - 97		8.1	7.7–22.4		638-1429	
Vertical 2	-20.5	86	7.4-109		4.8	0.31-5.78		343-656	
Sinking from Epilimnion				143-150			7.4-10.2		636-1129
Pre-1960 Burial				129			10.2		1011
Post-1960 Burial (south)				237			18.7		2559

Table 8.7A. Sum of annual N, P and Si inputs and outputs for Lake Malawi Nyasa.

	N	P	Si
Total Lake Inputs	540 - 773	16.3 - 20.8	699 – 1163
Total Lake Outputs	133 - 241	10.4 - 18.9	1024 - 2572

Table 8.7B. Sum of annual N, P and Si inputs and outputs for the epilimnion.

	N	P	Si
Epilimnion Inputs	510-742	20.7 – 38.1	1084 – 2158
Epilimnion Outputs	148 - 154	7.6 – 10.4	649 - 1142

Assumptions used in calculating nutrient inputs and outputs:

1. Dissolved N and P fluxes are based on TDN and TDP measurements, not inorganic N and P measurements.
2. All particulate Si fluxes represent “available” (readily soluble) Si, except for sediment burial rates, which are based on sediment biogenic Si measurements.
3. Due to the large degree of uncertainty in whole-lake N-fixation rates, N-fixation was not included in the calculation of N inputs.
4. The range of inputs accounts for the minimum and maximum estimates of river fluxes.

5. The range of outputs accounts for the difference between the pre-1960 burial rate averaged for two grab samples (north and south) and the post-1960 burial rate for the south.
6. Denitrification is not accounted for in the estimates of N output.

The Nitrogen Cycle – A comparison of the various nitrogen flux pathways (Fig. 8.5) reveals that rivers and atmospheric deposition are similar in magnitude as sources of new nitrogen to the lake. Therefore, both of these sources must be monitored if changes in nitrogen inputs are to be detected.

The nitrogen fixation flux presented in figure 8.5 is based on a volumetric fixation rate of $0.001 \text{ mmol N L}^{-1} \text{ hr}^{-1}$. If this flux is accurate, then nitrogen fixation is also a major source of nitrogen to the lake. While the rate of $0.001 \text{ mmol N L}^{-1} \text{ hr}^{-1}$ is lower than the rates for some experiments in November-December 1997, this rate was measured at a time of year when nitrogen-fixing cyanobacteria are generally most abundant, and it is possible that rates throughout the rest of the year are even lower. A comparison of total nitrogen inputs and outputs for the epilimnion (Table 8.7A; Fig. 8.5) indicates that, even if nitrogen fixation is ignored, the estimate of annual nitrogen flux into the epilimnion is greater than the flux out of the epilimnion. This imbalance would be exacerbated if the nitrogen fixation flux was applied, and it suggests that the lake may not rely heavily on nitrogen fixation as a nitrogen source. The intermittent presence of nitrogen fixing plankton, along with the observation that nitrogen fixation is not essential to balance the epilimnetic nitrogen budget, supports the earlier conclusion (chapter 6) that plankton production is controlled by a fine balance between nitrogen, phosphorus and light supply.

If a nutrient is conservative within the hypolimnion and metalimnion (i.e. does not undergo rapid changes in composition due to biological or geochemical reactions), then at steady state the flux from the hypolimnion to the metalimnion should be similar to the flux from the metalimnion to the epilimnion; i.e. whatever enters the metalimnion from the hypolimnion must eventually exit the metalimnion into the epilimnion. If the mean nutrient concentration for each stratum is used to calculate vertical flux rates, the hypolimnion-metalimnion N flux is $70 \text{ mmol m}^{-2} \text{ yr}^{-1}$, while the metalimnion-epilimnion flux rate is $23 \text{ mmol m}^{-2} \text{ yr}^{-1}$. This inequality is due to the fact that nitrogen is not conservative in the deep waters; it is lost through the process of denitrification (a process in which bacteria utilize NO_3^- as a terminal electron acceptor in the respiration process; this process occurs only in anoxic or hypoxic conditions). Denitrification converts NO_3^- to N_2 , which is generally not utilizable as a nitrogen source for bacteria and algae.

This denitrification is reflected in vertical NH_4^+ (ammonium) and NO_3^- (nitrate) profiles (Figs. 8.3 and 8.4). NO_3^- concentrations are typically low in the epilimnion, increase to a maximum of between 5 and $10 \text{ } \mu\text{M}$ in the metalimnion, and decline to 0 in the hypolimnion. NH_4^+ concentrations are high ($>20 \text{ } \mu\text{M}$) in the hypolimnion, but decrease rapidly at the hypolimnion-metalimnion boundary. NH_4^+ is a high-energy molecule used by chemosynthetic bacteria. The NH_4^+ profile reflects the bacterial nitrification of NH_4^+ at the oxic-anoxic interface (the biological oxidation of NH_4^+ to NO_3^- in the presence of O_2). This, along with the decomposition of settling particulate nitrogen, result in the production of NO_3^- within the metalimnion. While some of this NO_3^- may diffuse upward into the epilimnion, under the hypoxic conditions at the base of the metalimnion (Fig. 8.4), much of it is used in denitrification.

The minimum estimate of whole-lake nitrogen input is still greater than the maximum output estimate (Fig. 8.6). This imbalance is likely due to the fact that denitrification is not accounted for in the summation of outputs, and the difference between measured inputs and outputs serves as an index of the relative importance of denitrification as a nitrogen loss process.

As for the whole lake, the epilimnion also appears to be receiving more nitrogen than it is losing (Fig. 8.6), even if nitrogen fixation is ignored as an input. However, water column denitrification cannot account for this imbalance, since this occurs only near the oxic-anoxic interface, which is always well below the epilimnion at a depth of $\sim 200 \text{ m}$. One potential explanation for this imbalance is that it is real, reflecting a non-steady state condition during the study period. However, an imbalance of this magnitude would result in the accumulation of a large amount of nitrogen in the epilimnion, which was not observed during the study period. A second, more likely, explanation is deeper epilimnetic sediments. Relatively high concentrations of NO_3^- are often measured in the lower

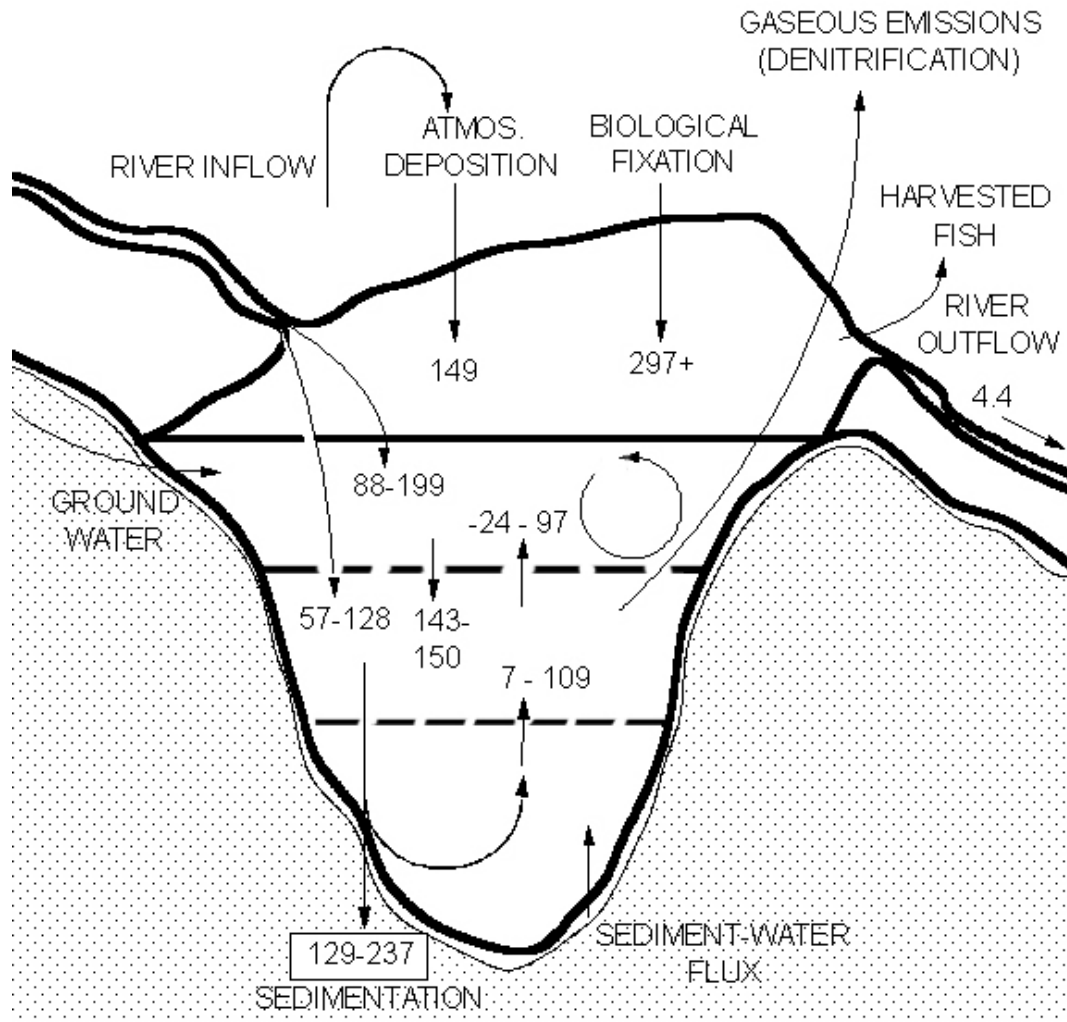


Figure 8.5. Nitrogen fluxes in Lake Malawi/Nyasa. All fluxes are $\text{mmol m}^{-2} \text{yr}^{-1}$, normalized to the lake's surface area.

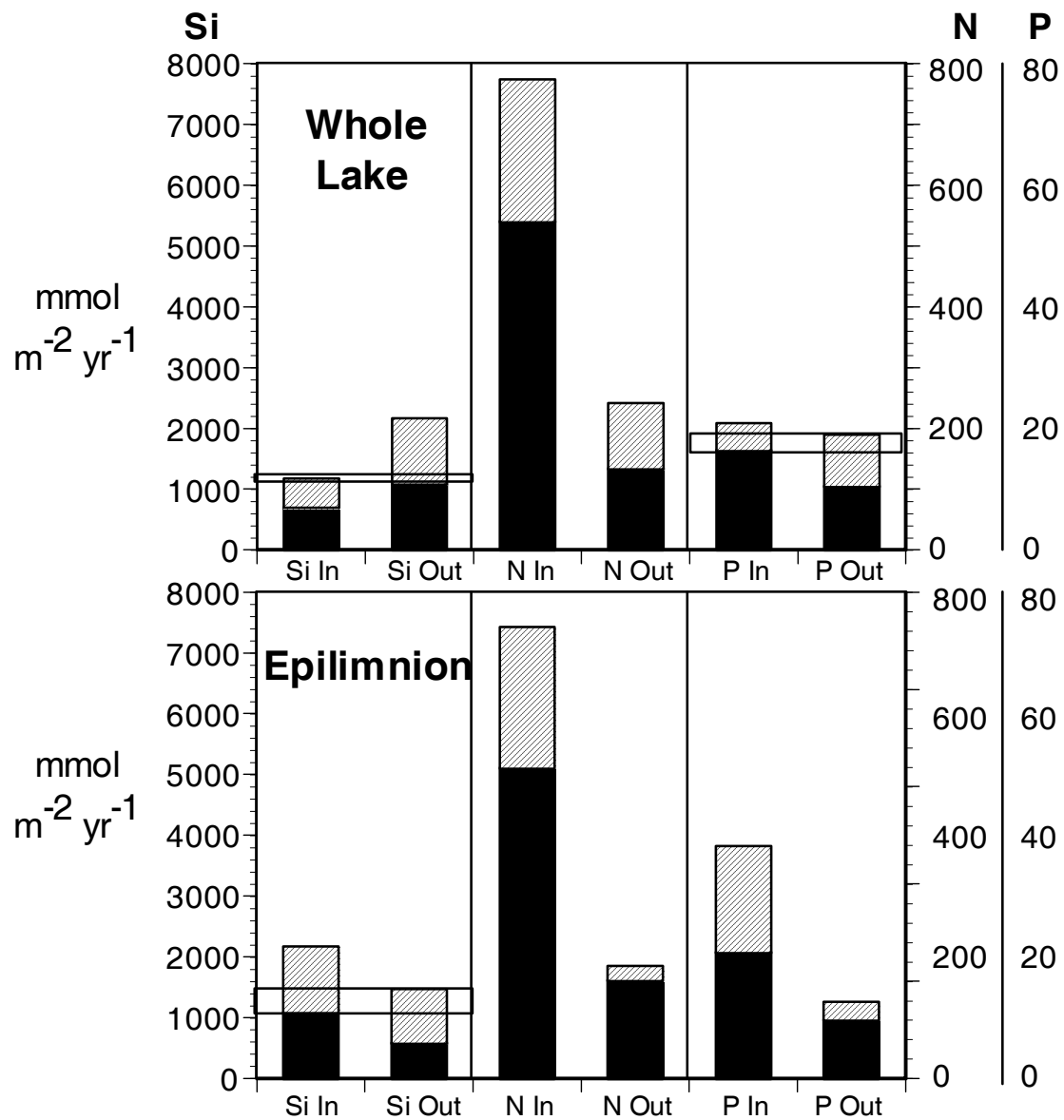


Figure 8.6 Estimated nitrogen, phosphorus and silicon fluxes for Lake Malawi/Nyasa. The range shown for each column represents minimum and maximum estimates. Where the input and output ranges overlap, the overlap range is boxed.

half of the epilimnion (Figs. 8.3 and 8.4), and denitrification near the sediment-water interface may utilize a significant portion of this pool. Confirmation of this process will require further experimental work.

For the purpose of predicting the lake's response to changes in nutrient input, an important question to address is whether or not the rate of denitrification will respond to changes in the inputs of other nutrients. Will increased nitrogen inputs be compensated for by an increase in denitrification rates, or will they result in increased nitrogen concentrations in the lake, as has been the case for the Laurentian Great Lakes (Bennett 1986)? These two alternatives can have profound effects on the plankton ecology and trophic dynamics of the lake. This issue is discussed in more detail below in the section comparing the different nutrient cycles.

The Phosphorus Cycle – For the whole-lake budget, phosphorus inputs and outputs agree quite well (Fig. 8.6). As for nitrogen, riverine and atmospheric phosphorus inputs are similar in magnitude for the whole-lake budget. While it is known that the atmosphere can be an important nitrogen source for aquatic ecosystems, very little attention has been given to the importance of atmospheric deposition in the phosphorus cycle. The deposition rate measured at Senga Bay ($7.9 \text{ mmol P m}^{-2} \text{ yr}^{-1}$) is 1.5 times that measured by Lewis (1981) near Lake Valencia (Venezuela), and more than an order of magnitude greater than that measured in some temperate regions (reviewed by Lewis [1981] and Bootsma et al. [1996]). Lewis (1981) and Bootsma and Hecky (1993) have suggested that a large portion of atmospheric phosphorus loading may be in the form of ash resulting from biomass burning, which is intense around Lake Valencia (Lewis 1981) and Central Africa (Andreae 1993).

For the epilimnetic phosphorus budget, vertical exchange is an important nutrient source, in addition to rivers and the atmosphere (Fig. 8.7). However, whereas previous estimates (Bootsma and Hecky 1993; Bootsma et al. 1996) suggested that the epilimnetic phosphorus budget was almost completely controlled by vertical mixing, the present results (which are based on a much more extensive data set) indicate that vertical exchange accounts for only about 50% of the annual phosphorus input to the epilimnion, with the remainder coming from the atmosphere and rivers. This has important implications when considering how the lake will respond to changed phosphorus loading. If vertical mixing is the main mechanism by which phosphorus enters the surface waters, the impact of an increase in riverine and atmospheric phosphorus inputs to the lake would be dampened or not noticed at all, at least in the short term. However, if a major portion of the phosphorus that supports algal production enters the epilimnion via rivers and the atmosphere, as our data suggest, then algal production and water quality in general will respond immediately to changes in riverine and atmospheric fluxes. The algal and sedimentary records suggest this may already be occurring, particularly in the southern portion of the lake (see chapter 7).

As for nitrogen, the estimate of epilimnetic phosphorus input is greater than the output flux (Fig. 8.6). Possible causes include: 1- An overestimate of riverine and atmospheric inputs; 2- An overestimate of vertical phosphorus exchange; 3- An overestimate of the fraction of river water that is retained within the epilimnion; 4- An underestimate of the phosphorus sedimentation rates and epilimnetic burial rates.

If atmospheric and riverine inputs are overestimated, then this will also put the whole-lake budget out of balance. The whole-lake phosphorus budget balances reasonably well (Fig. 8.6), but input is slightly greater than output. Therefore, new inputs may be slightly over-estimated, especially atmospheric deposition, which will probably be less over the open areas of the lake than near the Senga Bay shore where it was measured (see chapter 3).

The most likely cause of the imbalance in the epilimnetic phosphorus budget is an underestimate of the amount of phosphorus lost to sedimentation and burial in the sediments. The estimated sinking rate of 9.4 to $12.3 \text{ mmol m}^{-2} \text{ yr}^{-1}$ is based on sediment collections in 100 m sediment traps. However, re-suspension and lateral dispersion of epilimnetic sediments may result in the transport of a large amount of particulate phosphorus along the lake bottom. This flux would not be measured by the 100 m sediment traps. The potential importance of this mechanism is supported by the observation that the 180 m and 140 m sediment traps at Station THRM2 always collected more sediment than did the 100 m trap. This mechanism would also help to explain the observation that, for all three nutrients, the total flux out of the hypolimnion (via burial and upward flux) is approximately two times greater than the particulate sinking flux at 100 m. The measured deep burial and vertical fluxes can only be

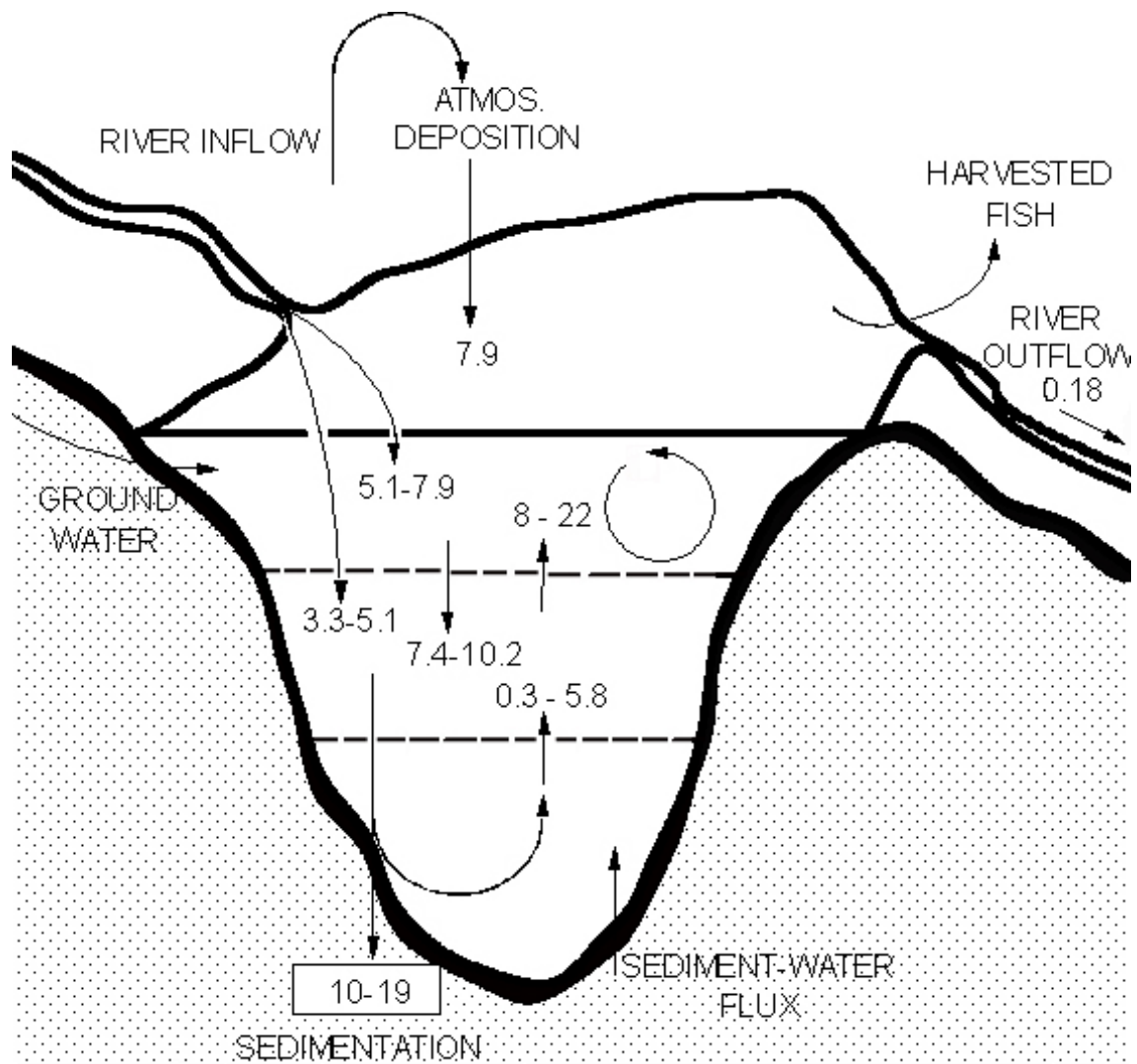


Figure 8.7. Phosphorus fluxes in Lake Malawi/Nyasa. All fluxes are $\text{mmol m}^{-2} \text{yr}^{-1}$, normalized to the lake's surface area.

supported if the estimated sinking flux is augmented by an additional flux, such as near-bottom flow of particle-laden water.

While some uncertainty remains as to the absolute phosphorus flux rates via various pathways, the close balance between total phosphorus inputs and outputs for the whole lake is a very encouraging result when compared with previous attempts to construct a phosphorus budget for Lake Malawi/Nyasa. This was one of the major goals of the nutrient flux studies. A balanced budget provides us with a degree of confidence sufficient to allow an assessment of the relative importance of various phosphorus sources.

The Silica Cycle – Almost all new silica entering the lake arrives via the rivers, with atmospheric deposition playing a very small role (Fig. 8.8). As for nitrogen and phosphorus, very little of this silica flows out of the lake; whatever enters the lake is ultimately buried in the sediments. For the whole-lake budget, the silica loss estimate is greater than estimated inputs (Fig. 8.6). However, the maximum input estimate is slightly greater than the minimum loss estimate, and therefore the budget can be considered to balance within the range of measurement uncertainty.

As for phosphorus, silica input to the epilimnion is controlled partly by new inputs (rivers) and partly by internal cycling (vertical flux from the metalimnion), with the latter being slightly greater in magnitude (Fig. 8.8). The vertical flux from the metalimnion to epilimnion ($638 - 1429 \text{ mmol m}^{-2} \text{ yr}^{-1}$) is greater than the flux from the hypolimnion to the metalimnion ($343 - 656 \text{ mmol m}^{-2} \text{ yr}^{-1}$). This is realistic, since the metalimnion-epilimnion flux will include SRSi that mixes into the metalimnion from the hypolimnion (assuming SRSi is conservative in the metalimnion) plus SRSi that is regenerated within the metalimnion and its sediments.

Interactions Between Nutrient Cycles: Prediction Scenarios

A regional comparison of river water quality (chapter 2) has indicated that, when normalized to catchment area and runoff, rivers flowing into the southern portion of the lake (Linthipe, Bua, Dwangwa) deliver a proportionally greater amount of dissolved and particulate nutrients than rivers in the central and northern regions. While further research is required to elucidate the links between catchment basin characteristics and river water quality, the data are compelling enough to cause concern about the impacts of changing land use on the water quality of the lake and its tributaries. The southern part of the lake's watershed has a greater population density (Bootsma and Hecky 1993), and less indigenous woodland than the central and northern regions (based on a 1993 land cover map produced by Satellitbild and the Malawi Forestry Department), providing circumstantial evidence that the regional differences in river water quality are related to differences in land use.

If the central and northern portions of the lake's watershed continue to experience population growth, deforestation, and increased agricultural intensity, then it is reasonable to expect that the water quality of rivers in these regions will become more like that in southern rivers. To determine what impact this might have on the lake, riverine nutrient loading was re-calculated by assuming that the discharge-weighted nutrient concentrations of all rivers were the same as for the Linthipe River. Under this scenario, riverine nitrogen flux to the lake would remain unchanged, while both phosphorus and silica inputs would increase by 1.7 X. For the epilimnion, riverine nitrogen input would not change, phosphorus input would increase by 1.22 X, and Si input by 1.35 X.

To understand what impact this will have on the lake's plankton community, the influence of nutrient ratios on algae must be considered. Different algal taxa have different optimal N:P and Si:P ratios, and the supply ratio for these nutrients can have a dramatic influence on algal community composition (Tilman 1981; Kilham and Kilham 1984; Kilham et al. 1986). While it is possible that a moderate increase in nutrient inputs may actually increase fish production (Stockner and Shortreed 1988), more algae does not necessarily mean more fish, since not all algae are of similar quality as a food source for zooplankton and fish.

As discussed above and in chapter 6, the lake's phytoplankton community appears to be poised between nitrogen and phosphorus limitation. An increase in the supply of one of these nutrients will result in the other nutrient becoming more crucial as a limiting factor, and algae that are more competitive for that nutrient will become dominant. Based on the estimates presented in figures 8.5 and 8.7, the present N:P loading ratio to the whole lake is 33 - 37, while the N:P loading ratio to the

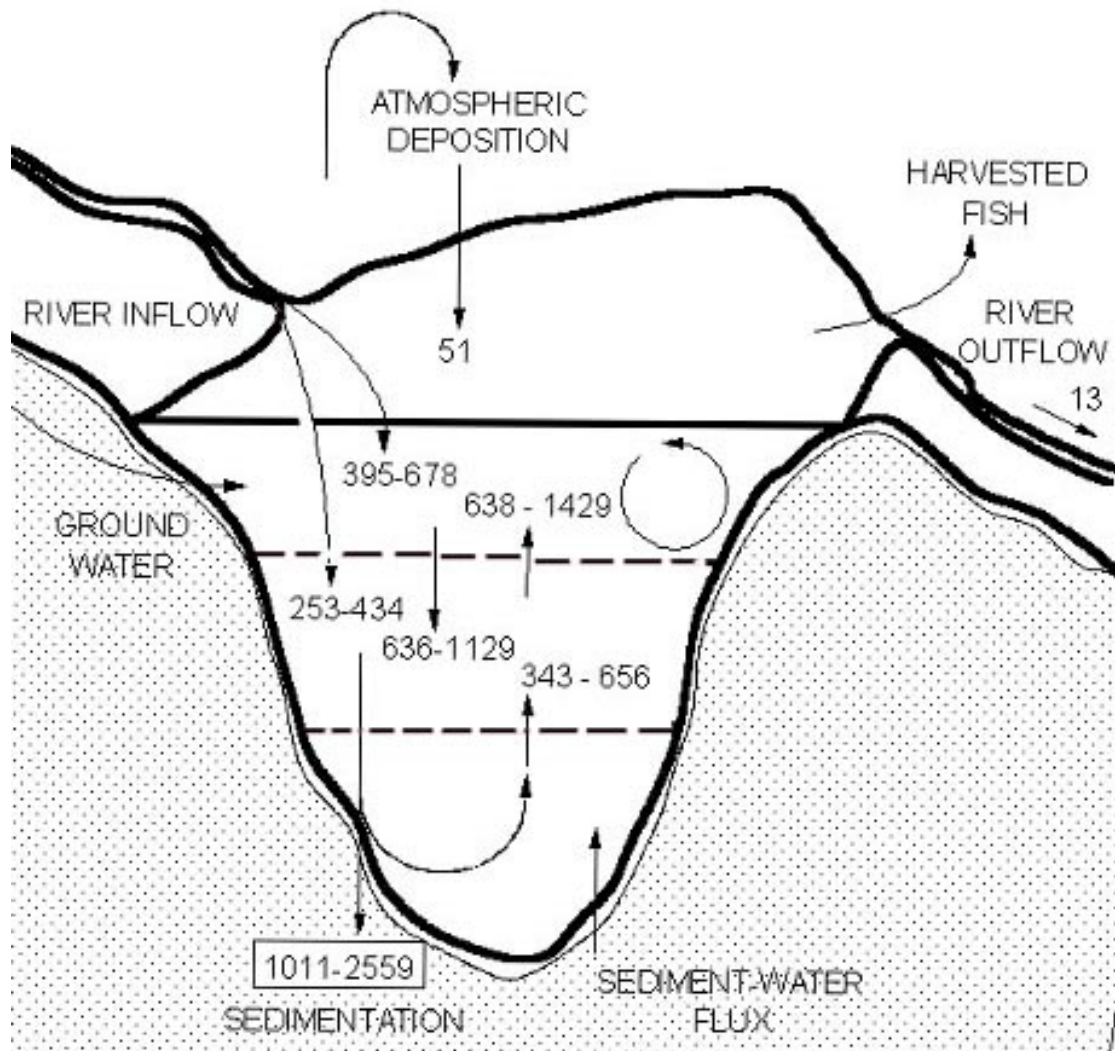


Figure 8.8. Silica fluxes in Lake Malawi/Nyasa. All fluxes are $\text{mmol m}^{-2} \text{ yr}^{-1}$, normalized to the lake's surface area.

epilimnion is 19 – 25, or 10 – 22 if N-fixation is excluded (the difference between the whole lake and the epilimnion is due to the low vertical dissolved nitrogen flux rate, which is a result of denitrification). The epilimnetic N:P loading ratio (excluding N-fixation) brackets the Redfield ratio (the ratio for a healthy, nutrient-replete phytoplankton community) of 16:1. Under the scenario of increased river nutrient fluxes, the N:P ratio for riverine loading would decrease from 17 to 9.9, and the epilimnetic N:P loading ratio would decrease from 10 – 22 to 8 – 18. Considering the phytoplankton community's present apparent balance between nitrogen and phosphorus limitation, such a shift can push the phytoplankton into a state of nitrogen deficiency. Under this condition, algal taxa that are more competitive for nitrogen are more likely to dominate. The best candidates are the nitrogen-fixing cyanobacteria (blue-green algae). While some tilapiines appear to be able to digest filamentous cyanobacteria (Moriarty 1973; McDonald 1987), they are generally considered to be a poor food source, particularly for zooplankton (Lampert 1981; Heerkloss et al. 1984; Haney 1987). Therefore, while larger phytoplankton feeders, such as chambo (*Oreochromis spp.*) may benefit from increased riverine nutrient fluxes, zooplankton and the food chain dependent on zooplankton (usipa, utaka, chisawasawa, ncheni) will suffer.

The Si:P loading ratio for the Linthipe River is almost equal to the mean Si:P loading ratio for all rivers. Whether or not the epilimnetic Si:P loading ratio would remain unchanged following increased nutrient inputs depends on the mechanism responsible for the increase. A comparison of regional Si:P ratios for rivers indicates that tributaries along the central portion of the lake's western shore have a much higher Si:P ratio than rivers at the southern and northern ends of the lake (Table 8.8). If increased phosphorus concentrations in rivers is the result of soil disturbance within the watershed, then this may be accompanied by increased silica mobilization through the dissolution of aluminosilicate minerals, in which case the epilimnetic Si:P ratio will remain unchanged. However, the silica concentration in rivers tends to fluctuate little, due to an apparent buffering mechanism (Edwards and Liss 1973), so that increased soil disturbance and weathering will not necessarily result in increased silica loading rates.

While it is uncertain whether an increased river phosphorus load would be accompanied by an increased silica load, if greater phosphorus loading is due to fertilizer application or biomass burning, this phosphorus will not be accompanied by silica, and the epilimnetic Si:P loading ratio will decrease. This will have profound implications for the phytoplankton community and for the cycling of all nutrients.

An important mechanism by which nutrients flow from surface waters to the metalimnion and hypolimnion is through the sinking of diatoms and zooplankton fecal pellets. Gardner et al. (1989) have shown the significance of this diatom shunt in Lake Michigan, and the sediment trap data of François et al. (1996) illustrate its importance in Lake Malawi/Nyasa. If epilimnetic phosphorus loading increases, diatom production will initially increase, causing increased sinking rates of particulate silica, along with other particulate nutrients. However, if the increased phosphorus loading is not accompanied by increased silica loading, the sinking and burial of diatoms will eventually result in lower dissolved silica concentrations in the surface waters. At present, surface water dissolved silica concentrations range between 5 and 25 $\mu\text{mol Si L}^{-1}$. The mean concentration for all surface samples collected between 1996 and 1998 is $14.2 \pm 3.2 \mu\text{mol Si L}^{-1}$. Evidence from ecosystem studies (Lund 1964; Kilham 1971) and laboratory studies (Kilham 1975) suggest that dissolved silica concentrations lower than this will result in a decrease in the relative abundance of diatoms. If the dissolved silica concentration in the surface waters of Lake Malawi/Nyasa declines, the production of diatoms and the sinking and burial of particulate nutrients can be expected to decrease.

The loss of a diatom nutrient shunt would have three potentially detrimental effects on the lake and its biota. First, because a greater proportion of organic decomposition will occur in the upper water strata, the retention of dissolved and particulate nutrients within the epilimnion and metalimnion may cause the water column oxic-anoxic boundary to become shallower. This would reduce the volume of water available for fish to live in, as has occurred in Lake Victoria (Bootsma and Hecky 1993; Hecky 1993). Shallow sediments would also become more anoxic, resulting in the loss of benthic organisms. Second, the retention of organic material and the loss of oxygen in the upper strata will likely result in increased nitrogen loss due to denitrification, promoting nitrogen limitation and the dominance of cyanobacteria. Third, the retention of particulate material (in the form of plankton and particulate detritus) within the epilimnion will result in greater water turbidity. While the effect this

Table 8.8. Si:P ratios (molar) for rivers along the southern, central and northern parts of the western shore.

River	Southern	Central	Northern
Linthipe	81		
Bua	89		
Dwangwa	36		
Dwambadzi		187	
Luweya		149	
Mlowe		133	
S. Rukuru			91
N. Rumphu			60
N. Rukuru			54
Lufira			97
Mean \pm St.Dev.	69 \pm 29	156 \pm 28	76 \pm 22

would have on the pelagic community is uncertain, it would certainly have a negative impact on the nearshore community, through reduced benthic algal productivity.

The time scale in which Lake Malawi/Nyasa will respond to changes in nutrient inputs can be determined by calculating the residence times of the various nutrients (determined as the mass of a nutrient divided by its input rate). The residence times for each nutrient in the whole lake and in the epilimnion (surface to 105 m) are given in table 8.9. While the whole lake will respond relatively slowly to changes in inputs (on the order of decades), the epilimnion can respond very quickly. However, while an increase in external nutrient inputs (rivers, atmospheric) will have an almost immediate effect on the epilimnion, a prolonged period of increased external inputs cannot rapidly be remedied by the abatement of inputs. The lake's hypolimnion is a nutrient storage tank, and hypolimnetic nutrient concentrations will increase if external inputs increase. Because of the longer residence times in the hypolimnion, and because a significant portion of annual phosphorus and silica flux to the epilimnion is from the hypolimnion, an increase in the lake's total nutrient mass will affect surface water chemistry, plankton dynamics, and trophic dynamics for years to decades after nutrient abatement.

Table 8.9. Masses, fluxes and residence times of nitrogen, phosphorus and silica for the whole lake and for the epilimnion. N* includes a nitrogen fixation rate of 219 mmol m⁻² yr⁻¹.

	Mass (megamoles)			Flux (megamoles/year)				Residence Time (years)			
	N	P	Si	N	N*	P	Si	N	N*	P	Si
Epilimnion	20655	1807	56184	8401	14853	797	42112	2.5	1.4	2.3	1.3
Whole Lake	104132	14178	766537	10031	16483	536	26557	10.4	6.3	26.5	28.9

Summary

1. The major sources of nitrogen to Lake Malawi/Nyasa are rivers and the atmosphere. Nitrogen fixation is also potentially important, both in the water column and in the littoral benthos. Most of the nitrogen that sinks out of the epilimnion is either buried in the sediments or lost as N_2 due to denitrification in the water column. The epilimnetic nitrogen budget suggests that denitrification in hypoxic water near the epilimnetic sediments may also be significant.
2. For the whole lake, rivers and the atmosphere are the main phosphorus sources. Vertical mixing is an additional mechanism of importance to the epilimnion. When compared to data from other parts of the world, atmospheric phosphorus deposition rates are among the highest recorded in the literature. A likely cause is the intense biomass burning that occurs throughout Central and East Africa. Within the lake, the lateral flow of sediment-laden currents is likely an important mechanism whereby phosphorus is transported from shallow to deeper parts of the lake.
3. Almost all silica entering the lake comes from its tributary rivers. For the epilimnion, both rivers and vertical mixing are important silica sources.
4. A regional comparison suggests that land disturbance within the lake's watershed results in increased riverine phosphorus loading, and possibly increased silica loading. Differences between catchment basin characteristics appear to have little effect on river nitrogen load. Rivers in impacted watersheds have lower N:P (and possibly lower Si:P) ratios than rivers in less disturbed watersheds.
5. Potential consequences of increased riverine and atmospheric phosphorus loading include:
 - a. a decrease in epilimnetic N:P and Si:P ratios.
 - b. a decrease in epilimnetic silica concentrations and in the relative abundance of diatoms.
 - c. greater retention of nitrogen and phosphorus within the epilimnion.
 - d. A shoaling of the oxic-anoxic boundary, reducing available fish habitat
 - e. dominance of the phytoplankton community by nitrogen-fixing cyanobacteria, with a negative impact on zooplankton and zooplankton-feeding fishes.
 - f. reduced water clarity, resulting in a shallower benthic trophogenic zone.
6. There are several indications that phosphorus input to the lake has recently increased. These include, lower abundance of the diatom *Aulacoseira* (possibly due to the stripping of SRSi from surface waters), an increase in the abundance of nitrogen-fixing cyanobacteria, and increased phosphorus and silica burial rates in the southern part of the lake.

Lakes are scavengers of nutrients. Through biological and erosive processes, nutrients in the rock, soil and detritus within a watershed are continually being lost from the terrestrial environment and entering the lake via rivers and the atmosphere. This is a natural process, but the rate at which it occurs can be accelerated by human activities around the lake. While changes in the chemistry and plankton composition of Lake Malawi/Nyasa have not been extreme to date, the changes observed, along with the imminence of further population growth, deforestation, and agricultural expansion, are compelling reasons to maintain a monitoring programme. With regard to nutrients, river and atmospheric monitoring is of greatest importance. As suggested in chapter 2, even the monitoring of suspended solids in rivers can provide information on whether conditions within catchment basins are changing. Within the lake, the phytoplankton are the most sensitive harbingers of change. In view of the wealth provided by the lake in the form of clean water, fish production, and the world's richest assemblage of freshwater fish, a simple, inexpensive nutrient and algal monitoring programme is a worthy investment.

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