Nutrient control of phytoplankton production in Lake Naivasha, Kenya

David S. Hubble[1],* & David M. Harper
Department of Biology, University of Leicester, Leicester LE1 7RH, UK
[1]*Ecological Monitoring & Research, 7 Ainsley Gardens, Eastleigh, Hampshire SO50 4NX, U.K.*
Author for correspondence. E-mail: dshubble@yahoo.com

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Abstract

Lake Naivasha, a shallow tropical lake in Kenya's Rift Valley, has an unstable water column and is moderately eutrophic. Nutrient (bottom-up) control of primary production is more important than grazing (top-down) control. Experimental nutrient enrichment was used to investigate bottom-up control in more detail. Minor nutrients were not found to be limiting, whilst nitrogen was more limiting than phosphorus with an algal preference for ammonium over nitrate. Sediments form a phosphorus sink but there is hypolimnetic release from the one area showing regular temporary stratification. This indicates that the rate of primary production in the water column could double if conditions change to allow lake-wide nutrient release from sediments. Both external and recycled nutrient regeneration are important.

Introduction

Lake Naivasha is a shallow freshwater lake situated in the eastern Rift Valley of Kenya, lying within an enclosed basin at an altitude of approximately 1890 m. Rainfall is bimodal with peaks in April and October, but shows inter-annual irregularity and annual evapotranspiration exceeds rainfall. There is one main inflowing river (Malewa) and a number of smaller, seasonal ones, but no visible outflow, although it is generally believed to have an underground outflow keeping it fresh. In common with many shallow tropical lakes, Naivasha is generally well-mixed (wind and convection) without persistent stratification in the main basin (Hubble, 2000). This creates a situation where algal cells undergo continuous vertical circulation which determines the prevailing light regime under conditions of intense solar irradiance. Lake Naivasha also experiences fluctuating water levels (Vincent et al., 1979) which influence its area, limnology and hence productivity (Becht & Harper, 2002). Recent human-induced changes have increased nutrient concentrations, and this has affected phytoplankton biomass (Hubble & Harper, 2002), so that the lake can now be considered moderately eutrophic with a state of 'endless summer' (Kilham & Kilham, 1990).

Nutrient (bottom-up) controls have been considered more important than top-down controls in tropical lakes, with nitrogen more limiting than phosphorus in Lake Naivasha (Talling, 1965). Concern about the effects of eutrophication and increased exploitation of water resources leads to the need to understand the control of phytoplankton primary production in order to accurately predict the effects of any changes. The objectives of the present study were to understand the present controls on primary production in Lake Naivasha.

Methods

Three study stations were used on the lake; a main lake station Hippo Point (HP); Malewa rivermouth (MR) close to the main inflow; and Crescent Island lagoon (CI), a partially separated crater within the main lake.

Light-dark bottles were incubated *in situ* at the three stations, at depths of 0, 0.5, 1, 2, 3, 5 and 7 metres usually for 1 h and the oxygen before and after measured by a B.O.D. probe on a YSI Oxygen meter (Yellow Springs, Ohio). The accuracy and repeatability of the method was found to be comparable to

the more normal titration methods (Hubble, 2000) but gave a distinct advantage in field measuring.

Experimental nutrient enrichment was used to investigate whether nutrient (bottom-up) control was more important than grazing (top-down) control. Experimental enrichments were made to incubation bottles, measuring productivity in mg C m^{-3} h^{-1}. Serial nutrient enrichment experiments were carried out in four different sets, each with a different nutrient. Four minor nutrients: silicon (as $Si(OH)_4$), manganese and chloride (as $MnCl_2$), iron and sulphate (as $FeSO_4$), and sodium (as Na_2EDTA) were tested. For each of these, a range of concentrations were added with the most enriched condition equating to the saturation level in Jaworski's medium. Four major nutrients: soluble reactive phosphorus (SRP), nitrate, ammonium and nitrogen (equal amounts of nitrate and ammonium added) were used. For each of these, samples were enriched with up to 10 μM of the relevant nutrient fraction prior to productivity incubation.

To investigate different nutrient pools, grazing dilutions were prepared and nutrients were added to produce three different conditions: +N+P (all nutrients added), –N (nitrogen as NH_4Cl omitted) and –P (phosphorus as KH_2PO_4 omitted). These experiments were run in pairs with one having the whole plankton community diluted, and the other only having the grazers diluted. Using productivity measurements to measure apparent growth rate, the contributions of 'Internal', 'External' and 'Recycled' nitrogen and phosphorus nutrient pools were calculated for each nutrient condition from the equation used by Andersen et al., (1991):

$$m(x) = {}^1/_t \cdot \ln[P_{(xt)}/P_{(xo)}],$$

where $m(x)$ = the apparent specific growth rate at dilution level x, t = time (h), $P_{(xo)}$ = initial productivity at dilution level x, $P_{(xt)}$ = productivity at dilution level x at time t.

Results

The minor nutrient series showed no response of productivity to enrichment, indicating that none of these nutrients were limiting (Fig. 1). This is especially important for silicon, as silicaceous diatoms are an important, often dominant, part of the algal assemblage in Lake Naivasha (Hubble & Harper, 2002). The major nutrients, nitrogen (separately as nitrate
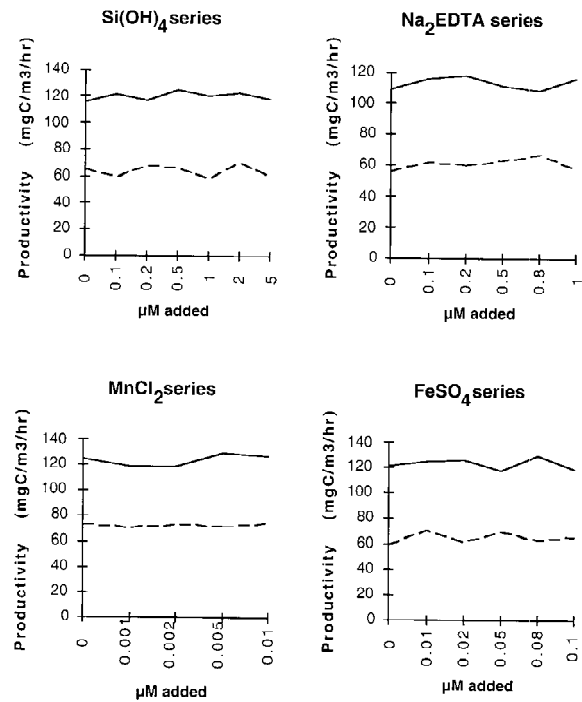

Figure 1. Response of primary productivity to enrichment of minor nutrients.
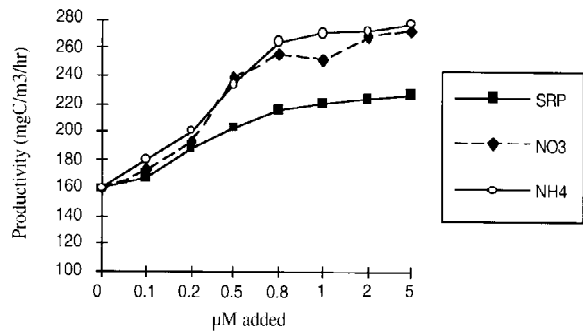

Figure 2. Response of primary productivity of surface lakewater to enrichment of major nutrients.

and ammonium) and phosphorus (as soluble reactive phosphate), produced a clear increase in primary productivity, with nitrate and ammonium increasing productivity more than SRP ($p = 0.005$ and $p = 0.003$ respectively) (Fig. 2).

There was an overall algal preference for ammonium over nitrate shown as higher productivity with ammonium enrichment ($p = 0.001$) as the latter requires more energy and the use of nitrate reductase. Productivity reached a plateau with enrichment of approximately 1 μM as nutrient levels became saturated given the algal population present.
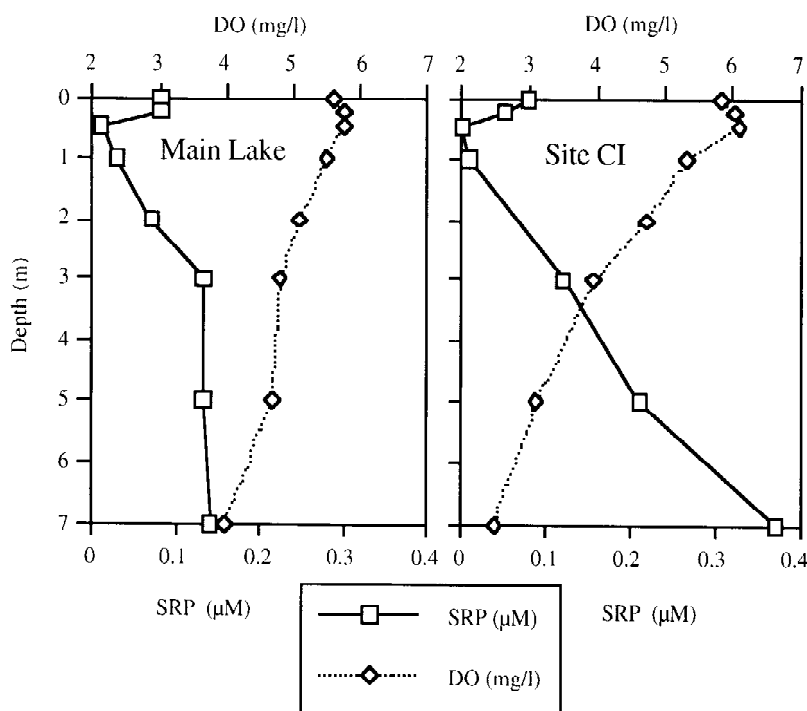
Figure 3. SRP & DO profiles at the main lake and Crescent Island lagoon, 21/10/98.

Experimental enrichments gave productivity responses under artificial nutrient conditions. The sediments form a sink for phosphorus (Kitaka et al., 2002), but the lake is well mixed (Hubble, 2000) and does not deoxygenate enough to release this store of nutrients. However, in the small Crescent Island lagoon, where the lake lies in a smaller volcanic crater, it is approximately 20 m deep and does stratify (Hubble, 2000). Here, hypolimnetic deoxygenation did occur (Fig. 3) and phosphorus was then released from the sediments, a process not seen in the main lake.

The main lake and the inflow showed little difference in the contribution of external (E) nutrients but the remaining productivity was mostly fuelled by recycled (R) nutrients at the inflow. In both cases there was little difference between nitrogen- and phosphorus-limited conditions with the fully enriched condition showing a greater contribution of internal (I) nutrients (Fig. 4).

In Crescent Island lagoon there was little difference between the contributions of nutrient pools under the three experimental conditions, whereas both the main lake and the inflow showed reduced 'Internal' contribution under the nutrient-limited -N and -P conditions, but increased 'Internal' contribution under the

+N+P condition. Changes in the contributions of the three nutrient pools occurred through variations in 'Internal' nutrient supply as the 'Recycled' and 'External' contributions remained equal (though variable) at all sites and under all conditions. For the +N+P condition, there was no significant variation between sites or pools, although inter-pool variation is greater ($p = 0.112$) than inter-site variation ($p = 0.839$). This is similar in both the –N condition ($p_{pool} = 0.077$ and $p_{site} = 0.816$) and –P condition ($p_{pool} = 0.132$ and $p_{site} = 0.764$).

Variation between conditions (for both absolute and percentage contributions) is indicated by two-tailed paired-sample t-tests at $p \leq 0.05$ for significance. There is a significant difference between +N+P and –N conditions for all cases except the 'Recycled' nutrient pool, which does not show a difference between any two conditions, as the rate of nutrient recycling by planktonic primary producers is extremely rapid, requiring only small quantities of nutrient unless a balancing nutrient is in excess, causing increased limitation. Hence the percentage contribution of the 'Recycled' nutrient pool does show a significant difference between conditions +N+P and both –N and –P, but not between –N and –P separately as both con-
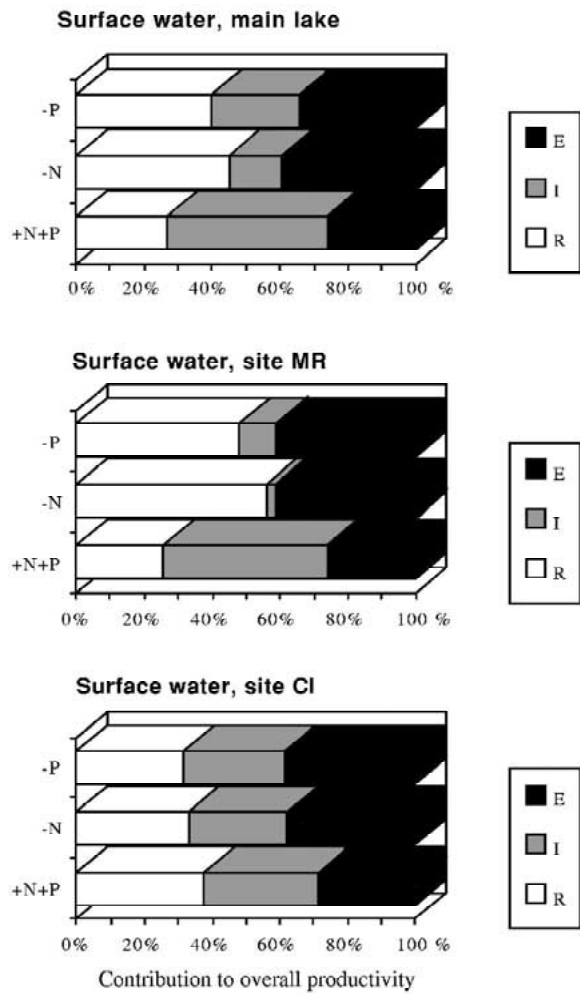
Surface water, main lake

Surface water, site MR

Surface water, site CI

Contribution to overall productivity

Figure 4. Separation of nutrient pool contributions to productivity in the main lake, Malewa River inflow (MR).

+N+P condition

-N condition

-P condition

Figure 5. Crescent Island lagoon profiles of nutrient pool contributions to productivity.

ditions experience opposite nutrient limiting effects. All other cases show significant differences except the percentage contribution of the 'Internal' nutrient pool between –N and –P, and absolute contribution of the 'External' pool between +N+P and –P. Considering each combination of two pools, significant differences are seen between pool contributions to productivity for all pairs, sites and conditions except between the 'Recycled' and 'External' nutrient pools in the main lake for the fully enriched +N+P condition. No significant inter-site differences are revealed. Crescent Island lagoon depth profiles (Fig. 5) show a peak of 'Internal' productivity at 0.5 m depth for the fully enriched and phosphorus-limited conditions. The nitrogen-limited condition shows a peak of 'Recycled' productivity at
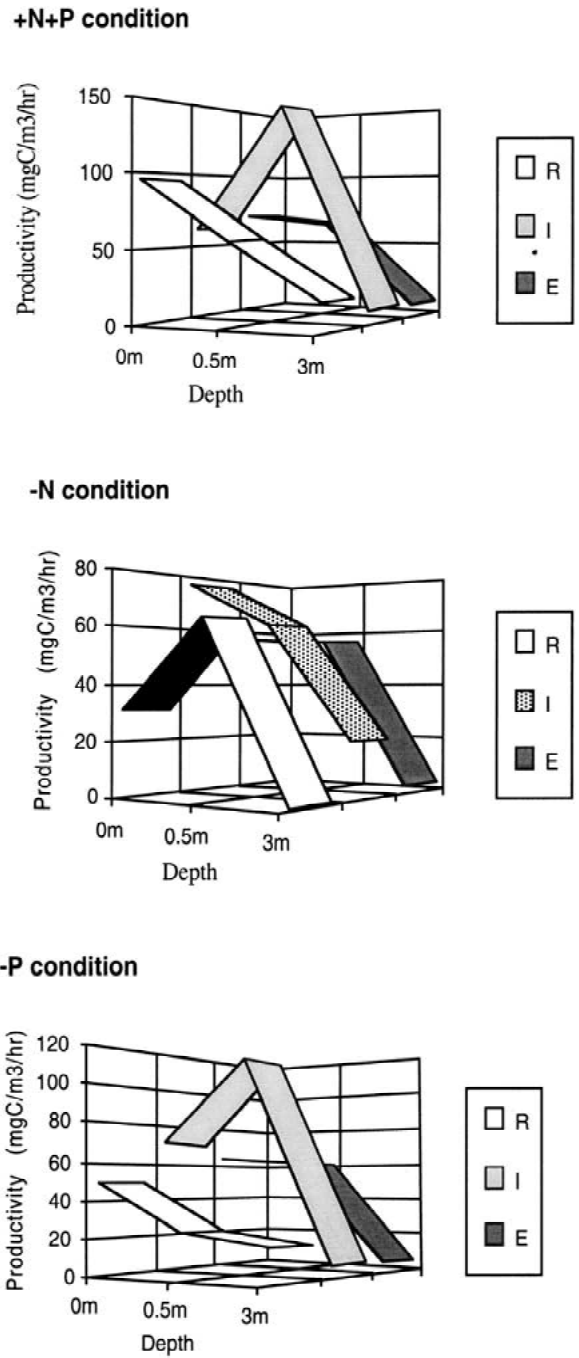
this depth although it is no higher than that of the other pools.

Separation of nutrient pools indicates that both 'External' and 'Recycled' regeneration are important, although further analysis will be required to link this

to energy flows through classic and microbial food webs. Analysis of inter-pool and inter-site differences between nutrient pools indicate that the variations in contribution of 'Recycled', 'Internal' and 'External' nutrient pools are not largely due to spatial heterogeneity within the lake despite differences in nutrient regime, hydrological conditions and sometimes overall productivity levels. Main lake and Malewa inflow sites showed little difference in the contribution of external nutrients but the remaining productivity was mostly fuelled by recycled nutrients at the Malewa inflow. This suggests that the effects of inflow is spread across the lake, and not merely confined to the river mouth. In both cases there was little difference between nitrogen- and phosphorus-limited conditions. Serial nutrient enrichment showed nitrogen to be more limiting than phosphorus and that ammonium was generally preferred over nitrate as a form of usable nitrogen. Productivity increase through nutrient enrichment varied between experiments but tended to reach a plateau at higher nutrient levels once saturation occurred, at which point a near doubling of productivity was often shown. This indicates the potential importance of nutrient release from sediments. This nutrient release does not appear, however, to have affected productivity either locally in Crescent Island lagoon or in whole lake terms, especially as any nutrient-rich waters from below 3 m in the lagoon would have been greatly diluted once transported elsewhere by currents in the lake. Even within the lagoon itself (diameter 1.3 km, depth 18 m) the water below 3 m only constitutes approximately 57% of the total lagoon volume (0.008 km^3) and thus this relatively nutrient-rich water would have been diluted by half if the lagoon mixed. Phosphorus resupply from sediments therefore occurs, but due to the lack of permanent stratification, is less important than water-column recycling.

Lake Naivasha underwent a 3 m depth increase during late 1998 and early 1999, and if this deepening continued, or wind-driven mixing became reduced, stratification could form more widely and with greater stability (Hubble, 2000). If this occurs, the resulting phosphorus release could accelerate eutrophication and increase productivity throughout the lake. There are a number of pressures upon the lake affecting the nutrient status (Johnson et al., 1998) including the development of intensive agriculture in the catchment right down to the lake edge (which removes the buffering papyrus fringe) and small-scale farming along the River Malewa increasing nutrient runoff.

Major nutrient input is due largely to riverine transport, with flow and nutrient load regulated by climatic and anthropogenic factors. The rivers Gilgil and Karati are seasonal depending on rains and show much smaller volumes of flow, but they may transport more concentrated materials than the Malewa (Hubble, 2000). Sediment is transported into the lake with a noticeable underflow (Hubble, loc cit) beneath the main lake surface waters as particles sink whilst still flowing away from the river mouth, especially during high rainfall – erosivity periods. Increased SRP levels lead to greater reduction in nitrate concentrations as phosphate enrichment occurs and nitrogen becomes limiting. The results of the experiments showing that the nitrate series correlated less closely with changes in SRP than changes in NH$_4$ indicate that the increased availability of nitrate due to enrichment outweighs some of the algal preference for ammonium. The concentrations of SRP in the lake indicate that, as well as differences in processes above and below the oxycline, there are processes causing variations in conditions within mixed layers. For instance at approximately 0.5–1 m depth there is maximal photosynthesis (Hubble, 2000) causing depletion of nutrients, often to zero or undetectable levels. Above and below this region, photosynthesis (and hence nutrient depletion) is reduced by photoinhibition and light attenuation respectively.

Discussion

Nutrient pool dynamics are more important in tropical lakes, especially in shallow waters, than temperate. Minor nutrients are not limiting, but may show variation with depth due to differential use by algae (Hubble, 2000). For example, silicates are partially depleted in areas of high diatom productivity (Talling, 1966), although this depletion is not limiting (Talling, 1993). Neither nitrate nor ammonium levels showed much difference between sites, remaining low (<20 μM) from the surface to 2 m depth, with a small steady increase below this as there was reduced algal activity and nutrient uptake due to light attenuation (Hubble, 2000). This effect outweighs that of mixing as the rates of nutrient uptake and cycling are greater than those of hydrological turnover (Hubble, 2000). As nitrogen fractions are transported in solution, not bound to sediment particles, any actual increase in nitrogen ions with depth (i.e., not merely a lack of algal utilisation) is likely to be due to settling of organic material,

or release of dissolved organic material from the lake sediments.

Much of the former papyrus fringe has been cleared from the northern shore (Harper et al., 1990), and so there is reduced buffering and consequently a gradient of reduced nutrient concentration moving away from the northern inflow of the River Malewa. In shallow water, wind, waves and currents lead to repeated resuspension of fine material (Knighton, 1998) and may contribute to concentrations at a given point, such as a *Ceratium* mass (122.5 μg L^{-1} chl *a*) at the Malewa inflow in May 1998 (personal observation). Once particles have settled, variations in fetch and depth affect wave generation and hence the resuspending shear stress at the lakebed (Giller et al., 1992). Reduced oxygen levels are found as sampling profiles meet the sediment–water interface (personal observation), however temperature reduction is sometimes detected without recording deoxygenation. Transects (Hubble, 2000) have shown that this occurs when an underflow of oxygenated water from the Malewa separates some relatively anoxic water from the lakebed which also has the effect of reducing temperature. These effects combine to partially determine vertical and horizontal variation in limnological parameters. The differences between enrichment series are seen at both low and saturated concentrations, at all sites and depths, and over time. This indicates that nutrient limitation is a major productivity control throughout the different conditions found in shallow tropical freshwater, assuming that Lake Naivasha is typical of such systems. Increased nutrient inputs both from changes in catchment land use via river inflow and sediment release therefore have the potential to greatly increase algal productivity and accelerate the processes of eutrophication. Although sediment phosphorus release currently occurs only in Crescent Island lagoon, if the lakewater becomes less oxygenated, there is potential for phosphorus to be released throughout the main lake basin. This situation may be more likely if nutrient inputs from the catchment continue to be enhanced by human activity and the lake becomes more eutrophic. Such concerns are applicable to many tropical lakes which are also vital water resources, therefore consideration of 'bottom-up' productivity controls may be an essential management tool.

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