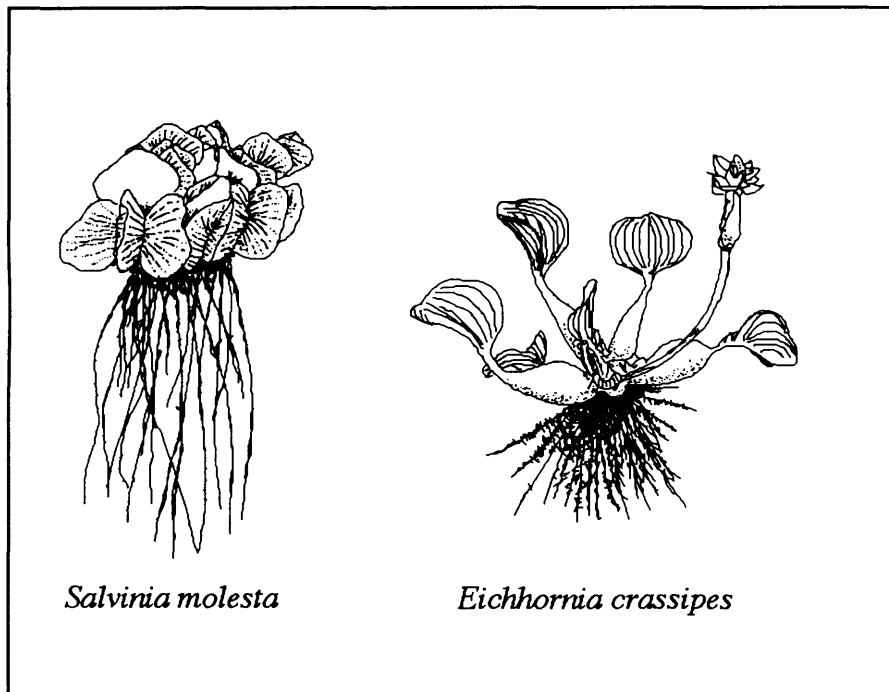


Controls on primary production in Lake Naivasha, a shallow tropical freshwater



Thesis submitted for the degree of Doctor of Philosophy at the
University of Leicester

by

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The laws of science contain no matter and have no energy either,
and therefore do not exist except in people's minds.

Robert M. Pirsig, *Zen and the Art of motorcycle maintenance*.



I ask Radcliffe, the last of my molecules, to bring me a model
and he brings me a model of the world.

Paul Ableman, *I hear voices*.



The only point of being here is to make a difference.
Anything less and you might as well be watching on TV.

Merrick, *Battle for the Trees*.



I find your lack of faith disturbing.

Darth Vader, *Star Wars*.

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Glossary of abbreviations used in the text

ANOVA	Analysis of variance
BOD	Biological oxygen demand
Chl <i>a</i>	Chlorophyll <i>a</i>
DCAA	Dissolved combined amino acids
DFAA	Dissolved free amino acids
DO	Dissolved oxygen
DOM	Dissolved organic matter
DON	Dissolved organic nitrogen
D _x	'Crossover depth'
FBA	Freshwater Biological Association
HNF	Heterotrophic nanoflagellates
HPF	Heterotrophic picoflagellates
IOS	Institute of Oceanographic Sciences
ISR	Incoming solar radiation
LD	Light-Dark (productivity incubation bottles)
LNGG	Lake Naivasha Growers' Group
LNRA	Lake Naivasha Riparian owners' Association
P:C	Productivity to chlorophyll <i>a</i> ratio
PCA	Principal component analysis
POM	Particulate organic matter
PP	Particulate phosphorus
SA:V	Surface area to volume ratio
S.E.	Standard error
SRP	Soluble reactive phosphorus
TDN	Total dissolved nitrogen
TN	Total nitrogen
TP	Total phosphorus
TSS	Total suspended solids
Z _{eu}	Euphotic depth
Z _{mix}	Depth of mixing

ABSTRACT

Controls on primary production in Lake Naivasha, a shallow tropical freshwater

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In many tropical lakes there is concern about the effects of eutrophication on ecosystems through pressures from land use changes and exploitation of water resources. It is necessary to understand the chemical, biological and hydrological bases of controls on primary productivity in order to accurately predict the effects of such pressures and develop relevant management strategies. Such controlling factors may be 'bottom-up' (e.g. nutrient limitation) or 'top-down' (e.g. zooplankton grazing). This study uses Lake Naivasha, Kenya as an example of a shallow tropical freshwater lake. In common with many tropical lakes it experiences fluctuating water-levels which influence its area and productivity, and is currently considered moderately eutrophic. Seasonality is determined by rainfall patterns, with diurnal changes greater than seasonal variations.

The light regime experienced by phytoplankton in Lake Naivasha dominates other controls as it determines the potential level of primary production. Photoinhibition reduces productivity by 25% at the surface with maximum productivity at a depth of approximately 0.5m. Light attenuation reduces productivity by 50% at 1m depth with zero productivity at 5m depth. Self-shading causes a 17% loss of productivity under conditions of below average productivity, but a 46% loss when productivity is above average. Hydrological factors form a primary control as the mixing regime determines the light regime. Lake Naivasha is generally well mixed, but where temporary stratification occurs there is nutrient resupply due to sediment anoxia. Without mixing, there is a 75% loss of productivity by cell sedimentation. Low sinking rates, tropical conditions and high nutrient availability favour low Surface Area:Volume species such as *Aulacoseira* which is the dominant genus. Changing conditions such as increased water-column stability could favour cyanobacteria.

Bottom-up controls were the most important in Lake Naivasha, reducing potential productivity by 50%. Nitrogen was found to be more limiting than phosphorus with an algal preference for ammonium over nitrate. Minor nutrients were not limiting. The main source of allochthonous nutrients was from river inflow with underflow and circulation around the lake. Top-down control by grazing imposes a 15% reduction in productivity with zooplankton preferring large 'production' cells over small 'standing-stock' cells. Grazers also prefer *Aulacoseira*, with cyanobacteria the least favoured food source. Smaller (< 65 µm) more numerous, faster-acting cells are more productive than larger forms. The tropical microbial loop was also investigated.

ABSTRACT (Kiswahili translation)

Matawala ya matoleo ya kwanza ndani Ziwa Naivasha, maji mbichi machache ya joto jingi

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Penye maziwa wa joto jingi ni shaka wa matokeo ya eutrophication juu mazingira kwa sababu ya mkazo natoka kwa madiliko ya kawaida ya nchi na faida ya maji. Lazima kuelewa msingi ya matawala ya matoleo ya kwanza kubashiri na usahihi matokeo ya hizi mkazo na kusitawisha maarifa ya vita ya maongozi. Hizi matawala wanaweza 'chini-juu' (e.g. mpaka ya nutrients) au 'juu-chini' (e.g. malisho ya zooplankton). Hii azimio inatumia Ziwa Naivasha, Kenya kama mfano ya ziwa mbichi machache ya joto jingi. Kama maziwa mingi wa joto jingi, na mageuzi ya kina ya maji. Hizi na uvutaji juu ya eneo na matoleo yake, na ya siku hizi ni sisana eutrophic. Kielezo ya mvua wanakaza nia majira, na madiliko ya siku zaida ya madiliko ya majira.

Ndani Ziwa Naivasha, nuru inashinda matawala mingine kwa sababu ya inakaza nia jumla ya kuwezekana baadaye ya matoleo ya kwanza. Photoinhibition inapunguza matoleo ya uso kwa 25%, na matoleo kipeo penye kina ya karibu sawa-sawa 0.5m. Kupunguza ya nuru inapunguza matoleo kwa 50% penye kina ya 1m na hapana matoleo penye 5m. Kivuli inapunguza matoleo kwa 17% na hali ya matoleo ya chini, lakini 46% kama matoleo ya juu. Elimu ya maji ni matawala ya kwanza kwa sababu ya kuchanganya pamoja inakaza nia jumla ya nuru. Ziwa Naivasha na kawaida wanachanganya pamoja wazuri, lakini kama tabaka-tabaka kwa muda tu inatukia, manufaa wa nutrients kwa sababu ya anoxia ya mashudu. Bila kuchanganya pamoja, sedimentation inapunguza matoleo kwa 75%. Haraka ya kuzama ya chini, hali ya joto jingi na kupatikana ya nutrients ya juu wanapendelea aina wa eneo ya uso: ukubwa ya chini kama *Aulacoseira*, aina mkuu. Hali kubadili kama imara zaidi ya nguzo ya maji, inaweza kupendelea cyanobacteria.

Ndani Ziwa Naivasha, matawala chini-juu muhimu wanapita yote, wanapunguza matoleo ya kuwezekana baadaye kwa 50%. Nitrogen iliweka mpaka zaidi ya phosphorus na upendeleo wa algae kwa ammonium juu nitrate. Nutrients kidogo zaidi sinaweka mpaka. Asili mkuu ya nutrients inatoka kwa maji ya mto, na mkondo wa maji chini na mzunguko kuzunguko ziwa. Matawala juu-chini kwa malisho inamuru kupunguza ya 15% ya matoleo, na zooplankton wanapenda zaidi asili kubwa 'matoleo' ya viumbe hai juu asili kidogo 'akiba' ya viumbe hai. Zooplankton wa malisho wanapenda zaidi pia *Aulacoseira*, na cyanobacteria kama wadogo kabisa kipenzi asili ya chakula. Asili ya viumbe hai vidogo zaidi ($< 65 \mu\text{m}$), wengi zaidi, upesi zaidi wanatoa zaidi wa maumbo kubwa zaidi. Kitanzi wa mikrobi wa joto jingi pia chini ya upelelezi.

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1. Introduction

In many tropical African lakes there is now concern about the effects of eutrophication on ecosystems through pressures from land use changes and exploitation of water resources. This problem at Naivasha (Figure 1.1) has been considered by Harper *et al* (1993) and requires management to reconcile possibly conflicting demands. This is particularly important as Lake Naivasha is designated by the Kenyan government as a wetland of international importance under the Ramsar Convention (UNESCO 1971).

Figure 1.1 Location map of Lake Naivasha.



Aquatic primary production can be considered as the mass of carbon fixed as newly grown organic material in the water column (units $\text{mgC}/\text{m}^3/\text{hr}$). It is necessary to understand the chemical, biological and hydrological bases of controls on primary productivity in order to accurately predict the effects of nutrient inputs and to develop management strategies which can protect ecosystem functioning. Some symptoms (both direct and indirect) of eutrophication include;

1. Algal blooms and surface scums.
2. Low transparency and loss of water volume by increased sediment accumulation.
3. Depletion of dissolved oxygen and development of nuisance biota.

Problems have been highlighted by studies on other lakes including Lake Victoria (Mugidde 1993) where land use intensification and population increase have led to changes in the food web through exploitation following earlier species introductions in the 1950s. These effects are coupled with changes in primary productivity by both top-down and bottom-up effects due to alterations in the nutrient regime. Acidification and water level effects may also cause problems for tropical lakes (Burrows 1990, Cooke *et al* 1993), with chemical perturbation a major factor under investigation.

1.1 Literature review: Tropical limnology

Nitrogen and phosphorus are the major nutrients controlling lake productivity. Talling (1993) notes that shallow African lakes often show high total phosphorus (TP) levels ($>30\mu\text{g/l}$) although most is particulate within algae, with a small rapidly recycled proportion present as soluble reactive phosphorus (SRP). Some lakes may show phosphorus limitation but Lake Naivasha appears to have an intermediate, fluctuating TP concentration (Talling 1993). This follows the general consensus that tropical lakes are primarily nitrogen-limited, but with little confirmatory work (except Kitaka 1991) at Lake Naivasha itself. The difference between transformations and transport of these two main nutrients lies in the fact that phosphorus is found in a sedimentary cycle whilst nitrogen circulates in soluble forms. Most phosphorus is bound as organic matter or in sediments, rendering it less available to producers and microconsumers through the following processes (Mitsch & Gosselink 1993);

1. The precipitation of insoluble phosphates with iron, calcium and aluminium under aerobic conditions.
2. The adsorption of phosphate onto clays, organic particles, and iron or aluminium oxides and hydroxides.
3. The incorporation of phosphorus into living biomass.

All nitrates are soluble and nitrogen exists in different oxidation states in lake water, the most important nutrient forms being nitrate (NO_3^-) and ammonium (NH_4^+) ions. Total nitrogen (TN) however includes insoluble matter and dissolved organic nitrogen (DON) includes amino acids. Nitrogenous forms are mineralised and interconverted by microorganisms including cyanobacteria which fix nitrogen using nitrogenase enzymes in heterocysts. As enrichment increases maximum but not minimum nutrient levels, potentially increasing the amplitude of any fluctuations and obscuring some minima by causing productivity (or biomass) peaks to merge. This response is more pronounced for nutrient fractions (SRP, NO_3^- , NH_4^+) than for total nutrient measurements (TP and TN) as the latter includes the pool contained within biomass.

1.1.1 Mixing regime and controls on primary productivity

The mixing regime is also of considerable importance to lake productivity as it determines the light conditions experienced by phytoplankton, especially as a shallow lake is likely to be well mixed, with occasional temporary stratification. Tropical nutrient cycling is also affected by the relatively large diurnal variation in environmental conditions compared with longer-term variations. This variation is dominated by the diel flux of short-wave insolation whilst interactions between the temperature, wind and depth regimes determine whether daily stratification develops. Such nutrient cycling occurs both in the water column and within sediments through sediment-water chemical exchange processes. Dissolved oxygen is the main variable used to investigate stratification as oxyclines are more clearly delineated than the often small temperature variations required to form a thermocline in warm tropical waters. This is because at tropical temperatures, small temperature differences cause large changes in water density. When the mixing rate is slower than the rate of phosphorus usage, there must be in-column recycling otherwise total depletion will occur as sediment resupply will not keep up with demand. If the water column recycling rate is fast enough, then sediment resupply will not be important unless there is stratification which disrupts

recycling into a euphotic hypolimnion. If stratification occurs there may be sediment phosphorus release due to deoxygenation and resulting iron-reduction (data from mixing and stratification measurements is required to investigate this process).

Work on temperate and marine waters has described microbial processes and pathways for energy flow facilitating the return of DOM, albeit inefficiently (Azam *et al* 1983), from phytoplankton release to the classic phytoplankton - zooplankton - fish food chain. These processes are termed the 'microbial loop' (Azam *et al* 1983, Carpenter 1988) although they have not been investigated in the tropics. Within the water column, the processes of nutrient cycling are interwoven with the microbial loop whereby bacteria are grazed by microzooplankton whilst phytoplankton are in turn grazed by macrozooplankton. This grazing activity can consume a large proportion of the material from primary productivity and may exert some significant 'top-down' control on the biomass of prey groups (Sherr & Sherr, 1994). 'Top-down' controls on phytoplankton biomass weaken however as overall production and algal biomass increase (Harris, 1994a). The tropical microbial loop is discussed in section 1.6.

'Bottom-up' (i.e. nutrient-based) controls form the basis for regulation of primary productivity through relative nitrogen and phosphorus levels with grazing activity mainly affecting carbon products. Bacterial activity may affect algal productivity through competition for nutrients (Caron, 1994). In eutrophic waters, algal biomass increases and sedimentation becomes a more important regulator than grazing (Harris 1994b). All nutrients can be limiting factors, but the reverse is not true, and more than one factor can be limiting at a time with respect to either *rate* or *yield* (Clymo 1995). Both nitrogen and phosphorus can therefore be limiting although the N:P ratio is more important than absolute concentrations when considering these nutrients alone, with a high ratio indicating P-deficiency. Phytoplankton are considered to form a "compound photosynthetic system" (Talling 1957), whilst zooplankton may now be seen as a "compound mineralising and synthesising system" through their nutrient cycling activity (Gulati *et al* 1995).

These systems are linked through rapid turnover within the P pools of zooplankton and phytoplankton, and slower exchange between the plankton and dissolved organic P pool (Salonen *et al*, 1994). These two processes are further complicated by any differences in contribution to overall productivity between small algae with high rates of activity, and less numerous, larger, slower algae. Nutrients are also resupplied from sediments during deoxygenation, which may occur if stratification develops. This process remains secondary whilst surface waters are being replenished through vertical circulation and mixing of allochthonous nutrients. Sediment-water interaction is more important in well-mixed shallow lakes where the sediment area:water volume ratio is larger, allowing a more active interface, especially if stratification and the associated hypolimnetic phosphorus and ammonium release occurs. Measurement of sediment concentration provided a rapid but approximate idea of relative nutrient loading between both lake and river sites as processes which increase sediment and other particulate matter are often associated with nutrient levels.

The algae of Lake Naivasha have been found to respond to enrichment of TP (Kalff 1983), although nitrogen is a likely limiting nutrient found at low concentrations in natural tropical freshwaters. The total pool of dissolved inorganic nitrogen (DIN) consists of ammonium and nitrate ions with low levels of intermediate nitrite compounds. Most nitrogen remains as ammonium in lakes if pH does not exceed 9.0, especially as decomposition depletes oxygen, releasing reduced nitrogen from organic matter (Wetzel & Likens 1991). The use of nitrates requires both energy and the nitrate reductase enzyme (Goldman & Horne 1983). Nitrogen fixation occurs through photosynthetic cyanobacteria, influenced mainly by oxygen concentration and light history in eutrophic lakes. If stratification occurs in eutrophic water, nitrate levels fall in favour of ammonium at the thermocline, affecting algal nutrient uptake. In the tropics, the ambient light climate is annually stable with high irradiance levels, leading to the idea of an "endless summer" (Kilham & Kilham, 1990). The greatest variation in irradiance is therefore due to the diurnal light cycle, although phytoplankton also

respond to longer-term patterns such as variations in seasonal rainfall and wind. This underlying long-term component leads to changes in runoff, mixing, inflow and nutrient input. Conditions favouring the dominant taxa involve an interplay between the factors controlling overall productivity (e.g. nutrient levels, general chemical and physical conditions, light regime) thus providing a variety of niches in a seemingly homogenous environment.

In lakes where the annual amplitude of seasonal changes is small, there may be long-term persistence of similar levels of biomass and species compositions as the biota are well-adapted to the stable conditions. If so, inter-annual variations become more important. This has been seen in earlier work at Lake Naivasha (Kalff & Watson 1986) which shows;

1. The seasonally-variable, fairly low biomass exhibited large inter-annual differences in the maximum:minimum biomass ratio.
2. The ratio could sometimes be predicted from the proportion of sediment surface in contact with epilimnetic water and followed the seasonal algal succession. This previously-accepted pattern states that from October to December there is a low biomass dominated by diatoms followed by an increase to an April peak accompanied by a shift to dominance by chlorophytes and then cyanobacteria until July.

1.1.2 Photosynthetic rate

Photosynthetic variation occurs through light attenuation and therefore incident solar irradiance and underwater light attenuation are the fundamental factors controlling the chlorophyll *a* (Chl *a*) content of shallow equatorial lakewater. For instance, if floating algae are not mixed away from the surface, photoinhibition of photosynthesis will occur causing the reductions in both photosynthetic rate and capacity which occur throughout periods of irradiance. Capacity reduction is a result of 'light-shade' adaptation with

potential photosynthetic capacity being greater early in the day when cells are shade-adapted, whilst true photoinhibition occurs through cellular damage by excess irradiance (Long *et al* 1994). The balance between photosynthesis and respiration (expressed as the P:R ratio) is described as a function of underwater climate and the relative rate of respiration. The daily net particulate production is only a small percentage of gross photosynthesis, with biomass and Chl *a* concentrations closely related to TP levels. The P:R ratio is positively related to Chl *a* and TP levels, but negatively related to water colour and dissolved organic carbon (DOC) levels, the latter influencing productivity through photosynthetic depression (del Giorgio & Peters, 1994).

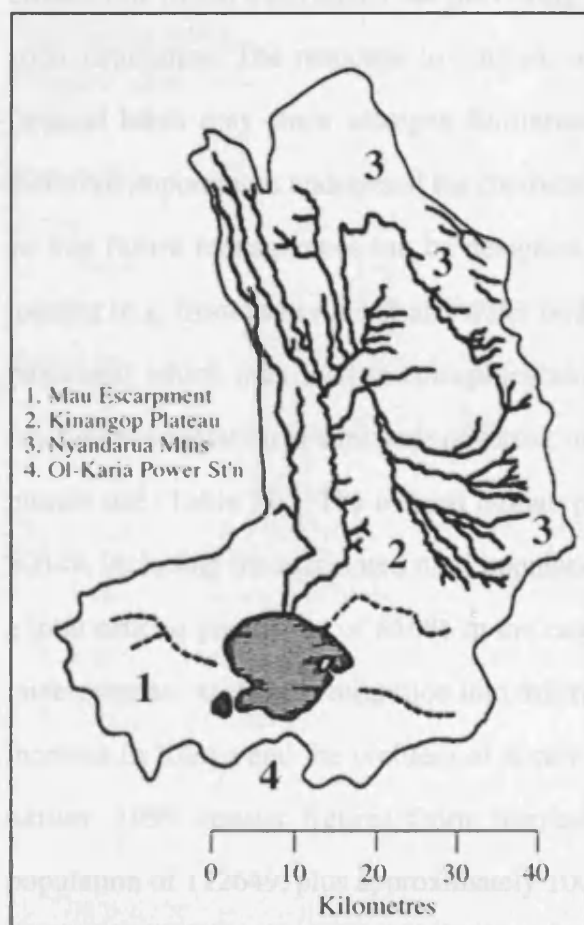
Degraded pigments include carotenoids and phaeopigments which may be measured by acidification to indicate pigment 'quality' as they are formed by Chl *a* degradation, either through subjection to darkness or passage through the gut of a grazer. Photosynthetic efficiency can then be calculated as photosynthetic rate per unit of Chl *a*.

1.1.3 Is Lake Naivasha a typical shallow tropical lake?

The term 'shallow' is difficult to define precisely but is used in this study to cover waters of a few metres depth where circulation reaches the bottom. Lake Naivasha is a shallow freshwater lake situated in warm and semi-arid conditions in the eastern Rift Valley of Kenya, lying within an enclosed basin at an altitude of approximately 1890m (Figure 1.2). Rainfall is bimodal with peaks during April & October but shows interannual irregularity and an annual evapotranspiration rate which exceeds local rainfall (Harper *et al* 1995). Lake Naivasha, in common with many tropical African lakes, experiences fluctuating water-levels which influence its area and productivity (Harper 1991). It also shows continually changing limnology through rainfall fluctuations in the catchment (Vincent *et al* 1979). Its limnology and productivity may also be affected by human intervention in the form of lakeside agriculture through papyrus clearance, drainage and application of fertilisers coupled with the effects of

species introductions (Harper 1991). These changes affect the aquatic plant ecology in terms of macrophyte species and distribution and phytoplankton biomass (Harper 1992a). Due to nutrient inputs, Lake Naivasha can now also be considered moderately eutrophic (Harper *et al* 1993). Before eutrophication in the 1980s it exhibited lower but more seasonally variable biomass compared with temperate lakes, with a seasonal shift between diatoms and cyanobacteria (Kalff & Watson, 1986). Three main rivers flow into the swampy northern section of Lake Naivasha and transport suspended sediments from upstream erosion during rainfall events. The River Malewa is the largest and flows continually with a watershed area of 1730 km² (Gaudet & Melack 1981). The rivers Gilgil (420 km²) and Karati (1240 km²) are seasonal depending on rains and their volumes of flow are much smaller.

Figure 1.2 Map of the Lake Naivasha catchment.



To determine whether Lake Naivasha is a typical shallow tropical lake, it is first necessary to decide if such an entity exists. Is it possible that shallow tropical lakes are only 'typical' at a very general level and other than this are so affected by variations in sediments and external factors that they are all different when considering more specific features? Consideration of Lake Naivasha as an example of a shallow tropical lake is important in order to determine how work undertaken there contributes to limnology in general, as opposed to merely providing information for a local management plan.

Shallow tropical lakes possess a number of distinctive features which control their general aquatic environment, and more specifically the productivity of such water-bodies in terms of the net rate of carbon fixation by phytoplankton. Firstly, shallow lakes tend to be well mixed by wind action and convection, lacking persistent stratification. This creates a situation where algal cells undergo continual vertical circulation which determines the prevailing light regime under conditions of intense solar irradiance. The response to nutrient loading is different to temperate areas as tropical lakes may show nitrogen limitation instead of phosphorus limitation. It is therefore important to understand the chemical and hydrological controls on productivity so that future management can be designed to take into account changes in nutrient loading (e.g. from farm runoff) and water budget (e.g. through abstraction for irrigation purposes) which may lead to eutrophication and reduced lake levels. The Naivasha catchment vegetation is a mixture of forest, wooded grassland, bushland, grassland and human use (Table 1.1). The official human population of Naivasha town in 1995 was 50349, including the associated rural population. Along with 35337 in Gilgil, this gives a total official population of 85686 in the catchment, although this will certainly be an underestimate as there is migration into this relatively affluent area, general population increase in Kenya and the problem of accurately performing a census in a developing nation. 1999 census figures from Naivasha Municipal Council indicate a total population of 112649, plus approximately 100000 uncounted as estimated by the Town Clerk (pers. comm.), and the population of Gilgil which is currently unavailable.

The water requirements for irrigated crops (mean m³/ha) range from 1310 for wheat to 1960 for vegetables with the rapidly expanding production of flowers needing 1890 (Huatuco 1998) as confirmed by S. Higgins (pers. comm.), flower farmer and Honorary Secretary of the Lake Naivasha Riparian Owners Association (LNRA). However, the extraction of water as a coolant for the expanding Ol-Karia geothermal power station uses as much as the entire local horticulture industry as confirmed by M. Mwangi, manager of Ol-Karia (pers. comm.).

Table 1.1 Malewa catchment land use January 1995 (Huatuco 1998).

Land Use type	Area (Ha)	% area of catchment
Wheat (irrigated)	231	0.07
Flowers (irrigated)	3598	1.09
Vegetables (irrigated)	2511	0.76
Alfalfa (irrigated)	728	0.22
Grass (irrigated)	285	0.09
Natural vegetation	4268	1.29
Rain-fed agriculture	135454	41.02
Forest	44430	13.46
Bare Soil	28367	8.59
Scrub	96125	29.11
Lava Flow	462	0.14
Water	12676	3.84
Settlement	1074	0.33
Total	330209	100.00

Comparing Lakes Naivasha and Oloidien (and patterns reported in other tropical lakes) with temperate lakes, (Kalff & Watson 1986), comparative analysis showed;

- i. A paucity of exclusively tropical algal species, with more than 30% of species found in both temperate and tropical lakes.
- ii. No evidence for a reduction in algal species abundance with latitude when moving towards the tropics as postulated by Lewis (1978b).
- iii. The proportion of nanoplankton is the same for temperate and tropical lakes.

- iv. Tropical seasonal and annual biomass oscillations seem as high as in the temperate zone, with Lake Naivasha showing large inter-year differences in the maximum: minimum biomass ratio.
- v. The average biomass ratio appears predictable for tropical lakes from the proportion of sediment surface in contact with epilimnetic water. Shallow, mixed conditions thus reduce annual biomass variation.
- vi. Overall, tropical and summer temperate phytoplankton composition and dynamics are fundamentally very similar, and therefore it is difficult to consider populations as totally separate from those at other latitudes.

1.1.4 Review of shallow tropical lakes: lakes George and Naivasha

Lake George, Uganda, shows little seasonal fluctuation in incident solar radiation and seasonal fluctuations in species composition and density are also small (Ganf 1974a). The diurnal cycle has an overwhelming effect on physical conditions and biotic activity. The lake is generally well mixed, although some temporary stratification may occur which is soon broken down by wind action (Ganf 1974b). There are very few wind-free afternoons on lake Naivasha and stratification outside Crescent Island lagoon is rare. Lake Naivasha is cooler than Lake George but both are partially fringed by papyrus with relatively short, narrow inshore regions. Both also have variable amounts of floating vegetation (Nile cabbage *Pistia stratiotes* on Lake George, Water Hyacinth *Eichhornia crassipes* and the floating fern *Salvinia molesta* on Lake Naivasha) and little submerged plant beds, although for very different reasons.

Considering the distribution of Chl *a* and species alongside stratification, Lake George had an exceptionally constant physicochemical aquatic environment (Greenwood 1976), high relative biomass of cyanobacteria (c.95%) and a 24-hour rather than seasonal physiological cycle (Ganf & Viner 1973). This leads to the presumption that tropical lakes are “stable” whilst “summer” conditions seem to especially raise the relative

anabolic rates of larger, low surface area:volume (SA:V) species. Net primary production was adequate to withstand the cropping rates and other losses and thus food did not limit herbivore growth. Daily nutrient demands were met almost exclusively by in-lake recycling. The concentrations of dissolved inorganic nitrogen ($< 10\mu\text{g/l NH}_3\text{-N}$) and phosphorus ($< 2\mu\text{g/l SRP}$) were very low, but silicon (20mg/l) and total phosphorus (200 $\mu\text{g/l}$) levels were relatively high (Ganf 1974b). It is however difficult to compare the nutrient status of lakes George and Naivasha due to the effects of ever-changing anthropogenic inputs which are investigated in Naivasha, but unknown at Lake George. The sediments are also easily stirred into the water column by mixing processes such as wave action. Gross photosynthetic rates were high (c. 12g $\text{O}_2/\text{m}^2/\text{day}$) whilst net production was relatively low (c. 1g $\text{O}_2/\text{m}^2/\text{day}$) because most of the carbon fixed was rapidly recycled via the respiratory cycle. Factors governing respiratory and photosynthetic rates therefore also regulate net production (Ganf 1970). Favourable light and temperature conditions along with bicarbonate use enhance photosynthesis, whilst high oxygen levels and self-shading tend to reduce it. Low net production and slow growth rates reduce overall N & P demand whilst the brevity of the mixing period may restrict species fluctuations (Ganf & Horne 1975).

Both phytoplankton and zooplankton in Lake George showed concentric distribution with highest concentrations in the centre, possibly due to the circular movements of the water mass, and/or grazing effects as fish showed the same distribution, although this could be directly due to the plankton distribution (Burgis *et al* 1973). Wave movements at the sediment-water interface disturbed much of the sediment down to approximately 14cm depth (Viner & Smith 1973), although this effect has not been investigated in Lake Naivasha. Examination has however shown that although the lake bed near Hippo Point is rocky, and that towards Crescent Island consists of stable sediments, most of the main lake shows a substrate of soft mud (Clark 1992). This implies a more gradual transition from water to sediment than more compact sediments with particles possibly in a colloidal suspension. Sediment deposition is correlated with lake level, with

deposition rates lowest when the depth is mid-range. In shallow lakes however, random distribution is the main mode of sediment transportation (Gibson & Guillot 1997).

Both lakes George and Naivasha are generally mixed due to their shallow, windy nature with Lake Naivasha being well-mixed apart from Crescent Island lagoon. This almost forms a separate basin during periods of low water and shows regular temporary stratification with the associated hypolimnetic deoxygenation and sediment phosphorus release (Melack 1979a). The main basin of Lake Naivasha is moderately eutrophic with nutrient input from river inflows and is less saline and less eutrophic than other Rift Valley lakes (Le Cren & Lowe-McConnell 1980). There may also be nutrient input from flower and vegetable farm drainage channels, and general runoff from small-scale agriculture and grazing in the catchment. This may be especially important given that much papyrus has been removed and land drained for agriculture (Harper 1991), hence it no longer provides such an effective buffering system (Harper *et al* 1993). There are also natural water level/lake area fluctuations on top of any anthropogenic effects from water abstraction for the purposes of irrigation and power station cooling. The freshwater nature of Lake Naivasha as opposed to the nearby saline lakes is an ongoing problem for a small army of hydrogeologists.

1.1.5 Comparison of Lake Naivasha with other shallow tropical lakes

Lake Ihema in Rwanda has the Akagera River as its single tributary and outlet, and the level of the lake is closely related to that of the river. It is situated in the Akagera National Park, and like Lake Naivasha is an important site for aquatic birdlife. Also like Lake Naivasha, the fishery revolves largely around tilapiines, with other less important species present. Both lakes show that increasing phytoplankton productivity has a direct positive impact on zooplankton (Mavuti *et al* 1996), with a lesser, indirect effect on tilapiines and aquatic birds.

Increasing the abundance of benthic producers would increase biomass of all groups except macrophytes which decline (probably due to nutrient competition). Detritus levels would thus increase, unless the rate of detritivory was sufficiently high. In Lake Naivasha this macrophyte reduction is assumed to cause a loss of crayfish (along with their predators such as bass and piscivorous birds, and the fisheries) but there is currently no supporting experimental evidence. This is a standard response to reduced food supply and does not imply that Lake Naivasha is a typical shallow tropical lake, especially given the great amount of human interference through species introductions and manipulation. There is a larger zooplankton population than seen in lakes such as Ihema and George due to eutrophication and the primary production is thus well utilised. Lakes Naivasha and Ihema however show similar biomass, production and utilisation of zoobenthos, all of which are lower in Lake George (Mavuti *et al* 1996). Biomass and Chl *a* are strongly correlated and coupled to TP levels. In Lake George, the algal biomass is dominated by diatoms, cyanobacteria and chlorophytes (Ganf & Horne 1975). Work by Kalff & Watson (1986) states that in Lake Naivasha, pyrrophytes are always present, and occasionally form a significant proportion of the algal community. Chrysophytes and dinoflagellates never constitute more than 5% of the total biomass, and October to December is understood to be a period of low biomass showing diatom domination with a subsequent increase to an April peak. This is accompanied by a shift in dominance to chlorophytes and finally to cyanobacteria, which remain until at least July. Work at Lake Lanao, Philippines (Lewis 1978a) and Lake Kinneret, Israel (Pollinger 1981) show how physico-chemical factors may affect algal and cyanobacterial community structure in tropical freshwater. This is described more fully in section 1.2.

Lake Baringo, Kenya shows a pattern of diurnal stratification probably accentuated by high turbidity and thus rapid attenuation of solar irradiance (Patterson & Wilson 1995). Mixing is re-established at night due to cooling and increased wind strength in the early evening. The phytoplankton is dominated by *Microcystis aeruginosa* with some associated epiphytes and concentrates (through buoyancy) in the narrow euphotic zone

during temporary stratification. During mixing, the phytoplankton are mixed throughout the water column and the diurnal cycle dominates over any seasonal limnological cycle that may exist. There is some evidence (in common with Lake George) of oxygen depletion below the diurnal thermocline although areal productivity is higher than that of Lake George ($1.0 \text{ gO}_2/\text{m}^2/\text{day}$) at $3.8 \text{ gO}_2/\text{m}^2/\text{day}$. In the subtropical lakes Apopka & Okeechobee, both in Florida, reactivity and bioavailability of phosphorus in lake sediments may be determined by different forms of phosphorus and their distribution (Olila *et al* 1995).

Some phosphorus reactions in sediments may be sensitive to changes in physico-chemical conditions such as redox potential and sediment resuspension. Phosphorus release and resupply processes are complicated by the different responses of the various phosphorus fractions present and their relative abundances. In fact, nutrient availability and seasonal fluctuations in nutrient supplies are often used to explain the control of phytoplankton abundance in tropical African lakes such as Lake Sonachi, near Naivasha (Njuguna 1988). The release of phosphorus from sediments is significant in shallow lakes because phosphorus concentration in the photic zone is directly affected and conditions for release can be ideal (Goldman & Horne 1983).

In the tropics, microbial activity is enhanced by the higher temperatures of sediments in such lakes and may lead to sediment anoxia with iron reduction and associated phosphorus release. High pH in the water column from photosynthesis may produce ligand exchange (OH^- for PO_4^{3-}) on iron-hydroxy complexes (Harris 1994b). Temporary stratification (polymixis), rapid development of anoxia and phosphorus release, followed by wind-induced mixing provide a series of internal loading events over a summer which must be especially important in a system under 'endless summer' conditions. Internal loading may also involve migration of cyanobacterial colonies from the sediment to upper waters, a process which may be important in shallow lakes.

Hydrologically a seepage system, Lake Naivasha is fresh due to its underground outflow, dilute inflows and bio-geochemical sedimentation of ions (Gaudet & Melack 1981, Ase 1987). Many other shallow tropical lakes exhibit a range of salinities including other fresh lakes (Talling & Talling 1965, Beadle 1974, Serruya & Pollinger 1983, Talling 1993) and the well-known highly-concentrated soda lakes famous for their populations of flamingos, such as Lake Elementeita, Kenya (Melack 1988).

For example, Lake Chad is a large endorheic lake which undergoes large variations in its depth and extent (Carmouze *et al* 1983). In the warmer season, diurnal thermal stratification occurs, with increased turbidity in drying periods due to sediment disturbance and phytoplankton concentration. Oxygenation conditions vary greatly over time and across the lake due to depth changes and variations in biological activity. Lake Kyoga, Uganda shows pronounced horizontal gradients in its chemical composition due to variable effects of the Nile inflow. The phytoplankton community is less diverse than Lake Victoria and is dominated by *Lyngbya* with other blue-green bacteria and green algae also important. The pH ranges from 7.6 to 9.0 with nutrient concentrations of 0.2mg/l NH_4^+ , 0.2mg/l NO_3^- and 0.52mg/l PO_4^{3-} (Serruya & Pollinger 1983).

In Tanzania, the freshwater Lake Kitangiri (conductivity 785 $\mu\text{mhos/cm}$, 64 mg/l Cl^- and 5 mg/l SO_4^{2-}) drains into the soda Lake Eyasi with 4366 mg/l Cl^- and 340 mg/l SO_4^{2-} . The pH is 8.0 to 8.9 and TP concentration has been measured at 1020 $\mu\text{g/l}$ (Serruya & Pollinger 1983). Near to Naivasha, Kenya's Lake Elementeita is fed by alkaline springs and has a pH of 10.9 and a chloride concentration above 4000mg/l. Similarly, Lake Natron, Tanzania is a highly saline lake with conductivity measured at 340000 $\mu\text{mhos/cm}$, 29000 $\mu\text{g/l}$ TP, 65000 mg/l Cl^- and 3100 mg/l SO_4^{2-} . Lake Nakuru, Kenya is characterised by an almost total absence of divalent cations, and in common with Lake Naivasha, a tendency to reduce and expand drastically, in some cases nearly drying out. The absence of outlets is one reason for its high salinity, with further salt concentration occurring due to its high watershed area:volume ratio and the

fact that it is fed by alkaline springs. It has almost no rooted macrophytes except in the north-west where freshwater streams permit papyrus (*Cyperus papyrus*) growth.

1.1.6 General properties of shallow tropical lakes

Overall, it seems that shallow tropical lakes are so affected by a variety of internal and external factors that they differ too greatly for any to be described as truly 'typical', with the possible exception of soda lakes which can be said to form a separate group. This contrasts with deeper lakes which are buffered against short-term events and those of small magnitude by their sheer size and volume of water which tends to 'dilute' perturbations to the system. Shallow tropical lakes do however share a number of characteristics, some of which are features of lakes in general. One example is the Lake of Guiers in Senegal which shares a number of features with Lake Naivasha such as seasonality driven by rainfall pattern, high invariable air temperature, and a turbulent water column (Cogels & Gac 1993).

In shallow tropical lakes, there are small annual variations in the light regime, but there can be daily thermal and density stratification producing vertical exchange barriers. This affects other factors in dynamic flux such as dissolved oxygen and pH which are influenced by interactions between photosynthesis, respiration, surface exchange, and phytoplankton concentration (Harris 1994b). Late in the day, any such stratification is ended due to reduced irradiance, stronger wind and cooling. Unlike temperate zones, tropical seasonality occurs in the form of rainfall patterns such as the bimodal monsoon system affecting Lake Naivasha, although lake-level fluctuations are not closely related to local rainfall (Harper *et al* 1990). In the dry season, evaporation exceeds outflow leading to an increase in ionic concentration, or salinity. Annual evaporation of 1360mm is also approximately double the mean annual rainfall of 610mm for Lake Naivasha itself although the wettest slopes of the catchment in the Nyandarua Mountains (also known as the Aberdares) receive 1525mm of rain (Ase *et al* 1986).

Some lake properties control or are controlled by phytoplankton biomass. The levels of biomass and organic matter produce high spectrally-sensitive light attenuation. Phytoplankton account for most TN and TP with inorganic N ($\text{NH}_4\text{-N}$ and $\text{NO}_3\text{-N}$) and SRP ($\text{PO}_4\text{-P}$) in small, actively overturned quantities. Bacteria and zooplankton also contribute to these fluxes and are involved in complex linkages through the microbial loop. Through higher pH leading to silicate leaching, tropical weathering also provides the relatively high silicon levels (Talling 1993) required to support an abundant diatom population. Shallow African lakes often have high TP levels ($> 30 \mu\text{g/l}$) which is a requirement for maintenance of dense, persistent phytoplankton (Talling 1993). Most TP is found as particulate phosphorus in phytoplankton, with fast turnover and a low concentration of SRP. Sediment-water exchange of SRP and ammonium is also enhanced by the high sediment area:water volume ratio, the short-lived nature of thermal barriers, and possibly by wind-disturbance of sediments. It may therefore be considered that shallower, smaller lakes are more likely to become eutrophic because they do not dilute incoming nutrients as greatly as larger, deeper lakes. There is also a smaller volume of water for potential deoxygenation through the activity of sediment organisms (Nedwell & Brown 1982).

Mixing and the light regime show a number of general properties linked with shallow tropical lakes. In surface waters, there is a diurnal oxygen increase and CO_2 decrease due to photosynthetic activity, whilst in deeper water this effect is reversed as respiration becomes dominant. The temporary nature of any stratification prevents hypolimnetic nutrient accumulation, with turbulence and diurnal cycles outweighing longer-term effects. As Talling (1993) states, changes over scales greater than 24 hours are generally small indicating exceptional stability within the lake system. Shallow lakes are therefore thermally distinctive through their lack of persistent stratification with mixing affecting the whole water column and well-developed daily cycles. Energy transfer is across the water surface therefore shallow water accentuates temperature maxima and minima, especially as energy consumption is often confined to the surface

by high turbidity. Turbidity and light attenuation are governed by particulate matter and dispersed 'colour' (*gelbstoff*) arising from heavy plankton development and the suspension of sediment and plant detritus. In waters shallower than 5m, turbulence disturbs bottom sediments leading to turbidity, especially after strong winds. High rates of photosynthesis are favoured, leading to diel fluctuations in O₂, CO₂ and pH, a process countered by lakes being optically deep. In this study, reviewing limnological theory and a range of case studies from shallow tropical lakes determined that such water bodies are only typical at a very fundamental and general level. Sediment and external effects are great enough to cause too much inter-lake variation for any to be truly considered 'typical' at any detailed level. The only systems which do seem to form a cohesive group are the soda lakes which can be treated separately. In conclusion, to show that Lake Naivasha is representative of other shallow tropical lakes, its 'typical' features may be summarised as follows;

1. Due to wind and convection processes, the entire water column is well-mixed with only temporary stratification, if any.
2. Tropical conditions cause diurnal variation to dominate over seasonal changes and for 'endless summer' conditions to occur. Thus any seasonal changes are linked to the pluvial system of the region.
3. Such summer conditions and the associated high zooplankton concentration mean that much primary production passes directly into the pelagic food web, reducing the bacterial role and favouring classical trophic links, an effect which can be tested through grazing experiments.
4. Nitrogen is expected to be the main limiting nutrient as opposed to phosphorus due to the effects of tropical weathering.
5. There is a high sediment area : water volume ratio which enhances the importance of any sediment-water interactions.

Tropical lakes can also be split into groups according to their mode of phytoplankton succession as described in section 7.1 (Melack 1979b).

1.2 Plankton community and succession

“In the sea and in most large inland waters, the bulk of living matter found in the open water is phytoplankton and hence the biological importance is immense; yet live plankton is only a very small part of the seston and the amounts vary.” (Round 1981). Estimates range from 1% (Holm-Hansen 1969) to 4.2% (Gillbricht 1952), yet this small fraction is responsible for primary production in the water column. It is itself affected in many ways by a complex interaction of factors, especially as there are a number of subdivisions within the planktonic lifestyle. For instance, meroplankton are those that spend part of each season resting on the sediments e.g. *Aulacoseira* and any species forming heavy sexual zygospores.

Unlike island species, the number of planktonic species does not increase with lake area. This may be because meroplankton are associated with sediments and therefore disadvantaged by greater size, and hence depth. Large shallow lakes should therefore have more species unless shallowness somehow constrains the euplankton (the permanent community of open water). Diversity, measured by indices such as Simpson's or Shannon-Wiener may also show successional patterns. Both of these indices show little effect of sample size, but whilst the Shannon-Wiener index is strongly influenced by species richness, Simpson's index gives more weight to common species (Spellerberg 1991). The Simpson's index was therefore chosen as *Aulacoseira* was expected to be the most common and important genus in productivity terms. Accounting for this importance was deemed more relevant than the influence of species richness. Richness is likely to fluctuate due to sampling as many genera were only found occasionally, although were presumably present at all times in low numbers.

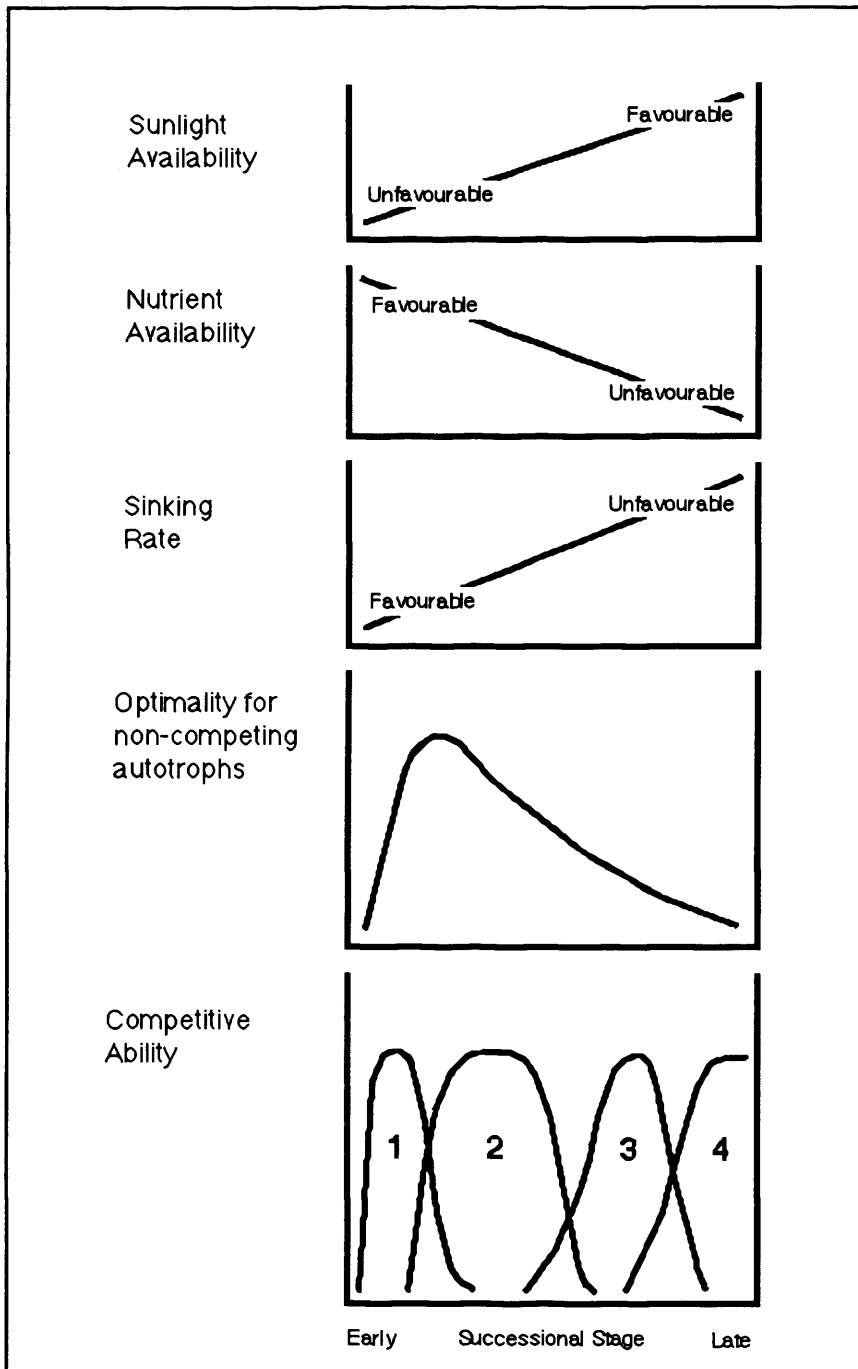
Algal communities (and hence their fluctuations) are often most conveniently categorised at the genus, rather than species, level with some groups conglomerated further such as flagellates and cyanobacteria. This is particularly useful if a group is

diverse and perceived to be important, but consists of species which are difficult to identify and/or found in low numbers (e.g. *Navicula*). Identification difficulties also arise due to variations in morphogenesis e.g. *Scenedesmus* may form easily misidentified unicells (Trainor & Schubert 1974), although identification to genus instead of species level for counting purposes helps alleviate problems caused by polymorphism. In the cyanobacteria, the concept of species is also without distinct boundaries (Chorus & Bartram 1999). Tropical lake phytoplankton populations show a number of general features such as planktonic forms which are benthic in temperate waters and lower species diversity than temperate waters, with chlorophytes tending to be dominant. Low alkalinity however favours *Aulacoseira* dominance as seen in Lake Naivasha during this study (section 3.1), and although they are superficially similar in a number of ways, lakes George and Naivasha have very different communities.

1.2.1 Control of algal succession in the tropics

In general, tropical lakes show cyanobacterial dominance during droughts and falling water levels and diatom dominance during periods of inflow and mixing (Harris & Baxter 1996) whilst rapid monsoon dilution may affect community structure as physico-chemical conditions are rapidly changed. The work of Lewis (1978a) on Lake Lanao in the Philippines gives a clear description of how a small number of chemical and physical factors may control succession in a deeper, stratified seasonal lake. For instance, a nutrient pulse leads to dominance by diatoms and cryptomonads once deep mixing is reduced sufficiently for cells to remain illuminated for net photosynthesis to occur. Then, during calm weather, nutrients are depleted and turbulence reduced leading to replacement by greens, then as the process continues, by cyanobacteria, and finally dinoflagellates as illustrated in Figure 1.3. Work at Lake Kinneret, Israel (Pollinger 1981) also indicates that low sinking rates and high nutrient availability are favourable as diversity increases during mixed and high nutrient periods, whilst it is minimal during periods of strong physical, chemical and biological stress.

Figure 1.3 Factors controlling phytoplankton succession (redrawn from Lewis, 1979).



- | | |
|---------------------------|--------------------|
| 1. Diatoms & Cryptomonads | 3. Cyanobacteria |
| 2. Chlorophytes | 4. Dinoflagellates |

This indicates that in early succession, low sinking rates (i.e. high turbulence) and high nutrient availability favour low SA:V species (e.g. *Aulacoseira*) whereas nutrient depletion and low turbulence favour high SA:V species (e.g. *Microcystis*) which can

scavenge scarce nutrients. This is seen both from palaeolimnology (Richardson & Richardson 1972) and more recently (Melack 1979b, Kalff & Watson 1986) in Lake Naivasha where there is an almost permanent early successional situation. This runs contrary to the generalisations by Margalef (1967) which suggest that high SA:V cells predominate in early succession due to their more rapid response to 'improved' conditions. As this early successional stage is generally present, such a rapid response is not required and this may explain why Margalef's progression towards dominance by high SA:V cells is not observed in a shallow moderately eutrophic lake like Naivasha. For temperate water, Trifonova (1988) provides an oligotrophic-eutrophic succession, with phytoplankton communities passing through a number of stages correlated with nutrient levels;

1. Oligotrophic stage. Chrysophytes and cold-water dinoflagellates are predominant with one annual maximum of productivity.
2. Several levels of mesotrophy. Diatoms predominate, with dinoflagellates, chrysophytes and cyanobacteria subdominant. There are two or three annual maxima.
3. Eutrophic stage. Cyanobacteria and dinoflagellates are predominant, chlorophytes and euglenophytes are subdominant.
4. Hypertrophy. Permanent high biomass with dominance by cyanobacterial species such as *Oscillatoria*.

Work in Sweden (Rosén 1981) has also shown that important physico-chemical factors in determining succession are pH, colour (not measured in Naivasha), conductivity, alkalinity, TN, TP and transparency. The work of Lind (1968) shows Lake Naivasha to be dominated by *Aulacoseira ambigua* but no explanation of phytoplankton periodicity was made, although for the Sasumua and Ruiru reservoirs in Kenya it was considered to be controlled by rainfall.

Species-specific requirements and preferences mean that successional control may be extremely complex, with subtle interactions between inflows, water column stability, overturns and the occurrence of dominant species. Individual species however, do not always respond according to their division or class. For example, poorly grazed large

forms such as *Oscillatoria bourrellyi* may act as sinks for nitrate through sedimentation, whilst better grazed species recycle ammonium as they are mineralised in surface waters (Heaney *et al* 1996). Phytoplankton communities may however experience both physical *instability* due to the mixed state of the water column and environmental *stability* as this mixing provides a certain light regime and prevents sedimentation loss. This form of 'continuous disturbance' is paralleled in ecosystems such as continually grazed grasslands where succession may be considered a function of 'vital attributes' (Noble & Slatyer 1980) although there are also non-hydrological factors such as chemical changes which may drive succession. For water-column phytoplankton during such a succession, these attributes may include;

1. Methods of arrival (e.g. inflow with river water).
2. Persistence (e.g. encysting or maintaining a small population).
3. The ability to establish in a developing community.
4. The speed of growth and cellular division.

It is also important to note that there is succession of form as well as community structure (Gibson 1975) as average filament length may change in colonial forms such as the cyanobacterium *Oscillatoria* and the diatom *Aulacoseira*. When considering successional controls, it may therefore be necessary to investigate the requirements of individual taxa, possibly as far as species level in the case of important dominant species. For example, cyanobacterial dominance is partly controlled by carbon dioxide levels (Shapiro 1997). Cyanobacteria generally have more efficient CO₂ kinetics than chlorophytes which means that although low CO₂ conditions are not required to initiate cyanobacterial dominance, these organisms tend to maintain their dominance by reducing it to levels available only to themselves. This suggests that, although cyanobacteria are not generally dominant in Lake Naivasha due to mixed conditions, the situation could change if long-term stratification occurred, and given the moderately eutrophic conditions found there, problematic blooms might occur. The importance of nutrients in determining community structure can also be seen where the transition from clear water to turbid phytoplankton-dominated conditions depends on the turnover of

limiting nutrients; a process which is retarded by macrophytes but facilitated by planktivorous fish and waterfowl (Romo *et al* 1996). The total amount of an ion may however bear little relationship to that available to algae. Dominant species show longer-term interannual changes superimposed upon the shorter-term seasonal successions and compositional fluctuations, although variations over both temporal scales appear to be greatly affected by climate. In Lake George, no succession was recorded (Ganf 1975), but in Naivasha it has been clearly illustrated (Kalf & Watson 1986). This may be the normal situation or merely temporary due to the recent interspersal of flood and drought conditions. Unfortunately earlier successional data does not exist to allow consideration of the historical situation, although the literature seems to form a general assumption that temperate waters should show more pronounced annual trends due to seasonality. This does not necessarily appear to be the case, although temperate successions may be more predictable, and Lake Naivasha may show underlying stability such as *Aulacoseira* dominance with many other species varying around it as a “focus”. Patrick (1997) also states that although similar species are found in temperate and tropical lakes, different ones dominate and may be found in different niches. For example, diatoms which are planktonic in the tropics may be benthic in temperate waters.

The magnitude, speed and complexity of limnological and associated algal community variations are brought into perspective by Hutchinson (1967) who states that the changes in climate and chemistry in a lake over one year are greater than those of soil climate and chemistry over millennia. For example, nutrients may affect species composition e.g. *Asterionella formosa* and *Cyclotella meneghiniana* can only co-exist when the growth of each is limited by a different nutrient (Titman 1976). Morphology is also affected by nutrients e.g. *Scenedesmus* forms spineless colonies when there is approximately 30 mg/l inorganic salts, and some strains are only colonial in dilute media, forming unicells which may be misidentified (Trainor & Shubert 1974). Similarly, unicellular taxa such as *Peridinium* may also change with nutrient enrichment through a reduction in cell size and duration with more active growth (Serruya & Pollinger 1977). The occurrence of CO₂, HCO₃⁻ or CO₃²⁻ as the predominant form of

inorganic carbon is correlated with the distribution of certain species in freshwater and thus species from acid (oligotrophic) lakes can be grown in water from alkaline (eutrophic) lakes if the pH is reduced (Moss 1973). Nutrient regeneration from phytoplankton is essential in chemical cycling, and occurs in a series of stages in the dark which is experienced by cells mixed permanently into deeper water or lost to sinking. During the first 24 hours there is either release or absorption of N and P, followed by a stationary phase for several days, and finally active nutrient release through decomposition for several hundred days. Approximately $\frac{1}{3}$ of initial N and P however remains undecomposed (Foree *et al* 1971). Eutrophication will affect the balance of species and increase overall production. As the process of eutrophication is currently occurring in Lake Naivasha, the community may be in a state of flux. Populations will also peak more often and/or at different times, thus causing succession changes. It is possible that growth peaks will merge allowing greater domination by one species. Considering temporal variation in abundance and composition of phytoplankton, overall abundance will be controlled by whichever resource/s is/are limiting and hence other types of pollution may have similar effects on species composition. Stable columns favour cyanobacteria and dinoflagellates, especially where $z_{eu} > z_{mix}$ whilst mixing favours diatom dominance; therefore diatoms suffer environmental stress if stratification occurs, zooplankton grazing (or other losses) increase or nutrients, particularly silicon, are depleted (Reynolds 1984). Previous Principal Component Analysis (PCA) work has thus shown that distinct periods of community change can be tightly coupled to changes in the physical structure of the water column (Harris, 1983). Succession in turbulent mixed layers is often due largely to changing physical conditions in surface waters as species may have critical euphotic depth (z_{eu}) : mixed depth (z_{mix}) ratios. In turbulent environments, there are a number of major features showing regular trends in the course of phytoplankton successions;

1. Reduced mixing and turbulence allows organised communities to be built upon, and is the driving variable.
2. Resource depletion, driving succession in a fixed direction by changes in the

availability of energy and/or nutrients, whilst a stable chemical environment leads to fewer species.

3. Productivity : Biomass ratios and efficiencies change so that in the initial stages there is more energy flow per unit biomass.

4. Changes in plant pigments accompany changes in physiology and species composition.

5. Grazing efficiency increases as selective grazing becomes more important.

6. DOC and detritus increase.

These features are interrelated through the reaction of organisms on their environment, and the effect of external perturbations on the whole system by non-chemical factors such as temperature and irradiance. Variations may be driven partly by niche diversification caused by species having different environmental optima. Effects such as these help to control the dynamic equilibrium between cyanobacterial/dinoflagellate and diatom dominance, however there are also factors influencing the sequence of summer dominance.

Firstly, the comparative rates of increase of different species will determine how quickly they respond to favourable conditions whilst the initial increases depend upon the relative sizes of inocula. Some species may build up populations on sediments or plants prior to release as plankton, but perennation is more common whilst resting-type spores may also accumulate before being brought into the water column. Resource gradients, especially among K-strategists, such as nutrient limitation and light regime also contribute to sequential control e.g. in tropical water, the greater density differences per unit temperature rise means gradients develop faster and approach nearer the surface. Similarly, the attenuation of different wavelengths due to absorbers of different wavelengths in water may affect species form, community composition and cell growth. The pattern of stratification and mixing may also have such effects with shade adaptation being linked to low temperature adaptation. Retention time may have an effect on populations through its relationship to loss factors which are in turn linked to the light regime via mixing (Round 1981).

1.3 Background conditions

In tropical lakes, circulation is a balance between wind-induced mixing and the stabilising action of solar radiation. If temporary stratification occurs, its stability is proportional to the thermal gradient. Whilst in temperate waters a thermocline needs a gradient of ≥ 1 °C/m, less is required in the tropics as water density decreases rapidly at higher temperatures. Full mixing will then be restored through a combination of increased wind strength and nocturnal cooling. The mixing regime is of particular importance as it determines the light conditions experienced by the phytoplankton assemblage, and therefore the dominant groups found at any time through a process of diurnal succession (Ganf 1974b, Harris 1983). For instance, fully mixed conditions favour diatoms and small chlorophytes which otherwise sink and are lost by sedimentation. Diatom-chlorophyte preference for mixing is especially relevant when considering a shallow lake as it is likely to be well mixed most of the time.

Temporary stratification may occur due to the diurnal cycle of wind and temperature with an increase in wind strength during the afternoon followed by cooling during late afternoon. Such stratification forms a vertical exchange barrier which is broken by reduced irradiance, stronger winds and the transfer of sensible heat to cooler night air. This leads to a situation of higher productivity in tropical lakes as diurnal temperature changes have a greater effect than annual variation (Talling 1993). The resulting limnological cycle should show the same main characteristics as temperate lakewaters but with its phases compressed to fit within a 24-hour period and a few metres depth (Talling 1993). Light attenuation compresses the photic zone, a process paralleled by increased volumetric photosynthesis. Integral photosynthesis meanwhile remains fairly constant as it depends on both these quantities, but is often well below the upper limit suggested by other factors (Krause-Jensen & Sand-Jensen 1998). This is because photosynthesis is restricted by light attenuation due to particles and DOM, both of which are prevalent in Lake Naivasha, contributing to its turbidity (Harper *et al* 1993).

In the upper illuminated layer, photosynthesis induces a diurnal increase of oxygen and decrease of CO₂, leading to higher pH and possible nucleation of solid carbonate whilst light respiration is 25 - 100% of dark respiration (Krömer 1995). Deeper in the water column, these pathways reverse as respiration dominates, but overall the effects are controlled both spatially and temporally by the regime of stratification and wind-induced turbulence. In shallow freshwater, a lack of prolonged stratification reduces NH₄-N accumulation in deeper waters. The wind also causes sediment turbulence leading to sediment-water interactions and a daily cycle of change is prevalent for many physico-chemical conditions (e.g. temperature, oxygen & pH) and biological activities (e.g. plankton layering and grazing). Nutrient resupply from sediments will occur, but is likely to play a secondary role to replenishment of the epilimnetic nutrient pool by water column circulation as regulated by evaporative cooling and the persistence of monsoon winds (Talling 1993). In shallow lakes, sediments may play a larger part than in deep lakes as they are in contact with a relatively larger volume of water which also increases hypolimnetic oxygen demand (Reynolds 1996).

Wind speeds greater than 2-3 m/s (as experienced daily in Naivasha) are required to mix floating algae away from the surface, and also regulate horizontal distribution (Webster & Hutchinson 1994). This determines the light regime experienced by algae and therefore the nature of the dominant assemblage as non-floating species require mixing to prevent loss by sinking. During periods of temporary stratification however, anoxic conditions may develop rapidly in the hypolimnion with an associated release of “reductant-soluble phosphorus” (Mitsch & Gosselink 1993) from the sediment through iron reduction before mixing is re-established. The sediment-water exchange of phosphate and ammonium is therefore enhanced by;

1. High sediment area:water volume ratio.
2. Short-lived nature of thermal barriers.
3. Wind-disturbance of sediments.

A layer of oxidised mud at the sediment-water interface may also act as a barrier preventing soluble ferrous phosphate from diffusing out of deeper anoxic regions, but its effectiveness depends on the level of consolidation and water content of the sediment (Jones & Bowser 1978).

1.4 The importance of climate

Climate is of prime importance to the ecology and overall environmental conditions of any lake. Wind and ISR together determine the mixing and light regimes through turbulence and convection as well as temperature. Through inflow of water and associated materials from the catchment, rainfall influences lake level and physico-chemical conditions, notably turbidity which in turn determines the light attenuation profile of the lake. The level of relative humidity also affects evapotranspiration rate, although this always exceeds annual rainfall on Naivasha. These few factors therefore have large and wide-ranging effects on primary productivity and the ecology of the producers as nutrient levels, wind-induced mixing and primary production are closely interwoven (Kalff & Brumelis 1993).

At the surface, excessive solar radiation induces photoinhibition of photosynthesis causing a reduction in rate. This is coupled with the reduction in photosynthetic capacity as cells become 'light-adapted' during periods of irradiance. Photoinhibitory cellular damage by excess irradiance (Long *et al* 1994) may also be coupled with the process of photorespiration reducing overall productivity. Such effects are based on the ambient light climate which is characterised by being annually stable with high irradiance levels in the tropics, leading to the idea of an "endless summer" (Kilham & Kilham, 1990). These effects also occur in the temperate zone, but are greater in the tropics. Again, this causes the greatest variation in irradiance to be due to the diurnal light cycle, although phytoplankton also respond to longer-term patterns. Further photosynthetic variation occurs with depth through light attenuation due to particulate matter and dissolved *gelbstoff*, producing an extinction coefficient as a function of wavelength. The levels of

solar irradiance and underwater light attenuation are therefore the fundamental factors determining the potential primary productivity (and hence biomass) of shallow tropical freshwaters. This is also important for macrophyte communities as the increased turbidity associated with eutrophication causes loss of macrophytes as emergent plants are outcompeted for light by phytoplankton (Harper 1992b).

Lake level changes can have profound effects upon an ecosystem as illustrated by the work of Serruya & Pollinger (1977) at Lake Kinneret. This site displayed a rapid reduction in level, resulting in the following chain of events. Firstly as volume decreases faster than area, there is more energy input per unit volume leading to faster heat transfer, coupled with a lower thermocline and decreased hypolimnetic volume. Decay of organic matter and sediment nutrient release thus occur in a smaller volume, and produce higher concentrations. Increased CO₂ concentration may increase the solubility of salts such as calcium phosphate whilst vertical convection facilitates the oxidation of benthic particulate organic matter (POM) and organic phosphorus, thus increasing SRP release. Once such processes combine to increase overall nutrient levels, algal communities show increased development of species with higher nutrient requirements. These processes therefore link lake level and climate with community composition, nutrients and inorganic carbon concentrations.

1.5 Zooplankton productivity controls

Zooplankton play a dual role in the nutrient fluxes of lakes (Hessen *et al* 1992), although bacteria may also be important;

1. A source of regenerated nutrients.
2. On a seasonal scale, a net sink, removing nutrients from the epilimnion in some proportion to their population mortality losses.

It is necessary to know the pools of zooplankton N and P to fully understand these roles. The ratio of recycled elements (C:N:P) depends not only on that in the seston, but also on the composition of the zooplankton community (Hessen & Andersen 1992). The composition of zooplankton affects the phytoplankton community by its absolute and relative release of dissolved elements along with grazing effects. For example, in Lake Washington (Lehman 1980) epilimnetic zooplankton supply 10 times more P and 3 times more N to the surface-mixed layer during summer than enters from all external sources. Remineralisation of nutrients through egestion and excretion can therefore provide a significant proportion of daily phytoplankton requirements. For this reason, ambient pools of dissolved nutrients can remain small whilst turnover rates are rapid. For grazers there are feedback mechanisms via the elemental constituents of algal food.

Through “rapid, coupled cycling of nutrients among phytoplankton, zooplankton, and the dissolved pools” grazers can therefore affect the chemical environment of phytoplankton (Sterner 1990). The role of zooplankton as a net source or sink of any given nutrient depends on its relative abundance in the food and grazers (Urabe *et al* 1995). Zooplankton may also regenerate nitrogen as ammonia (Dugdale & Goering 1967), although only as a relatively small fraction (c.10%) of the total used by phytoplankton. Recycling of N and P may be decoupled (Elser & Frees 1995) such that either may be produced separately.

Nutrient limitation and grazing controls on phytoplankton communities are both important and have shown temporal patterns in non-stratified lakes (Hansen *et al* 1997). Such grazing can affect temporal patterns of algal pigments in suspended and sedimenting algae (Poister *et al* 1999), which is especially important if dominant species are preferred prey items. Nutrient limitation is the more important factor during summer conditions, but grazing impact is partly determined by zooplankton community structure, with cladocerans and rotifers providing significantly greater top-down control than cyclopoid copepods. Zooplankton predation may also exert considerable direct

grazing pressure on phytoplankton, even in situations of feeding saturation, and this is the activity which induces 'top-down' control. Zooplankton also prey upon protozoa, especially those smaller than 20 μm , but this is assumed to have no significant impact upon 'top-down' productivity controls (Carrick *et al* 1991). The methodological ideas proposed by Landry & Hassett (1982) and Andersen *et al* (1991) are utilised to investigate such grazing controls.

1.6 The tropical microbial loop

A number of aspects of the microbial loop can be related to the conditions found in Lake Naivasha, and to shallow tropical lakes in general. Within the water column, the processes of nutrient cycling are interwoven with the complex microbial loop whereby bacteria are grazed by microzooplankton which, along with phytoplankton, are in turn grazed by macrozooplankton. The zooplankton then release bacterially-available nutrients and organic matter through processes such as excretion and 'sloppy feeding'; incomplete ingestion, digestion and absorption of food (Weisse 1989). This causes a 'short-circuit' in the traditional microbial food chain as energy flows from zooplanktonic consumers to bacterial producers for biomass production (Azam *et al* 1983). Heterotrophic flagellates of both pico (0.2 - 2 μm) and nanno (2 - 20 μm) size classes (HPF & HNF respectively) are thought to be the main consumers of bacteria including bacterial production (Simek *et al* 1990). The extent and pathways of transfer of microbial production to higher trophic levels are largely unknown as the microbial loop has not been investigated in the tropics. Larger zooplankton do not impact greatly on pelagic organisms however, although they do predate the flagellates which are the major bacterial grazers (Turner *et al* 1988). Through the processes of zooplankton nutrient release and bacterial grazing, most energy channelled through the microbial loop is produced and consumed by organisms of sizes smaller than 20 μm .

Theoretically, the microbial loop should be less important in more eutrophic waters because the larger input of nutrients to the system means that primary production does

not rely on recycled nutrients. Even if DOM is not channelled through the microbial loop complex to higher trophic levels, there should not be substrate exhaustion through sedimentary loss of organic matter (Weisse 1989). Substrate exhaustion would otherwise occur in oligotrophic systems with high energy input and rapid organic matter cycling where primary production is largely based on recycled nutrients. Zooplankton contribute to nutrient cycling through excretory release of ammonia and phosphates, although the rate of production will depend on the P content of food and ultimately on environmental nutrient levels (Vadstein *et al* 1995). Through excretion and photo-oxidative cell damage, phytoplankton release low molecular-weight carbon compounds such as glycolic acid and some peptides which are utilised by bacteria (Hellebust 1965). These in turn produce algal-available forms of phosphorus. In this way, the carbon and nutrient flows within the microbial community are strongly interlinked. Such linkage shows dynamics arising from three main processes which have the potential to facilitate growth and production of all components of the pelagic community, although with reduced importance in eutrophic waters (Carpenter 1988);

1. Commensalism via the production of DOM by phytoplankton and its subsequent use by bacteria.
2. Competition for nutrients between bacteria and phytoplankton, as influenced by substrate availability.
3. Predation by flagellates, ciliates and microzooplankton, providing a mechanism for the feedback of nutrients and some DOM. This is important as bacteria tend to outcompete phytoplankton for nutrients, and these substances would otherwise have the potential to be tied up in bacterial biomass.

1.6.1 The role of zooplankton

Grazing should balance bacterial production under 'permanent summer' conditions by cropping up to 162% (average 79%) of this production (Sanders *et al* 1989). Grazing may therefore be expected to maintain a uniform concentration of bacteria. HNF are

expected to be dominant in this role (Simek *et al* 1990), but little is known about the role of rotifers, ciliates and cladocerans in freshwaters so this view of HNF grazing dominance may change as such work progresses. Size fractionation may be important as HNF show size-selective grazing, consuming larger dividing cells (i.e. 'production'), rather than smaller 'standing stock' (Simek & Straskrabova 1992). This has implications for overestimation of bacterial productivity which, if grazing is size-selective, can only be described as biomass, not cell numbers. Variation in both grazing activity and productivity is on a diurnal rather than seasonal scale due to the lack of seasonality in the tropics. This conclusion is supported by the following evidence;

1. Previous studies show productivity controls to vary mainly over a diurnal scale due to the dominance of the daily light regime (Talling 1993).
2. Zooplankton grazers show daily vertical migration related to diurnal patterns of fish predation and location of food supply (Lewis 1979). Zooplankton grazing impact varies with season in temperate waters (Sanders *et al* 1989) but in the tropics no such seasons exist.

There may however be important short-term events (such as temporary stratification) or localised nutrient sources (such as littoral sediments). Bacterial production is however offset by losses such as sedimentation, lysis, viruses, predatory bacteria and antibiotics (Simek & Straskrabova 1992), and is therefore conservative over both seasonal and diel cycles (Simek *et al* 1990) with grazing as the dominant bacterial loss factor.

In general, bacterial production and abundance are highest in the meta- and hypolimnion during summer stratification events. In temperate lakes, bacterivores can graze more than the total bacterial production in spring when productivity is low. Production however exceeds grazing losses in summer, a situation which would be expected to occur in the 'endless summer' conditions found in tropical regions. Grazing is positively coupled to bacterial abundance, with HNF accounting for up to 99% of

bacterivory (Sanders *et al* 1989). Protozoa can thus process a significant proportion of photosynthetic and bacterial production in aquatic environments, with bacteria in turn utilising the DOM released by protozoa. By releasing DOM, grazers and bacterivores channel primary production to bacteria, where DOM is recycled. The bacterial use of DOM short-circuits the microbial loop, increasing the efficiency of nutrient regeneration (Nagata & Kirchman 1992). There is also an important link to nutrient dynamics in that bacteria prefer released DOM to ammonium whilst phytoplankton prefer ammonium to nitrate. Where DOM and/or nitrate is/are available, conflict is therefore reduced in the use of nutrients for productivity between phytoplankton and bacteria.

1.6.2 The microbial loop in Lake Naivasha

The model proposed by Taylor & Joint (1990) does not support the microbial loop hypothesis and shows bacteria to be unimportant. It suggests only a small transfer of carbon from bacteria and protozoa to higher trophic levels with little effect on nutrient cycling. It states that heterotrophic bacteria act as a carbon sink (i.e. not a transfer system) in pelagic food webs. There are a number of reasons why the microbial loop might be of reduced importance in lakes such as Naivasha;

1. Tropical 'summer' conditions reduce the effectiveness of the 'short-circuit' by which bacteria utilise DOM and increase the efficiency of nutrient regeneration (Azam *et al* 1983).
2. Allochthonous nutrient inputs and eutrophic conditions both reduce the importance of such regeneration as there is no substrate exhaustion (Weisse 1989). The importance of the nutrient release caused by intensive grazing is therefore reduced in eutrophic waters.
3. 'Summer' conditions and the associated high zooplankton concentration mean that most primary production passes directly into the pelagic food web, reducing the bacterial role and favouring classical trophic links. The role of bacteria as a nutrient sink is reduced in eutrophic waters or in conditions maintaining sufficient zooplankton for

most primary production to pass directly into the pelagic food web, as is seen during 'summer' conditions (Rheinheimer 1991).

4. Grazing balances bacterioplankton production, maintaining a uniform bacterial concentration by cropping all or nearly all of this production (Sanders *et al* 1989). This should be especially true as the bacteria capable of photosynthesis cannot cleave water, and being obligate anaerobes, do not grow well in oxygenated waters such as a well-mixed shallow lake. In eutrophic shallow lakes, cyanobacteria may dominate however, and have previously done so in Lake Naivasha (e.g. Kalf & Watson 1986).

5. In shallow eutrophic lakes, increased pH in interstitial water may occur due to high algal assimilation near the lake sediment surface, resulting in soluble P release and reducing the necessity for efficient regeneration (Tunney *et al* 1997).

Following this consideration of both 'top-down' controls on productivity and the role of microbes, there are a number of ways in which grazing can be linked to the microbial loop;

1. Much phytoplankton production is released as DOM, and this pool is enhanced partly by zooplankton excretion, being used by pelagic bacteria for their biomass production. In nutrient-rich waters, many zooplankton feed on bacteria which have previously degraded considerable quantities of organic matter (Rheinheimer 1991).

2. Whether or not grazing exerts significant control on productivity depends on the relative importance of the contribution of grazed organisms to total productivity as well as the presence of certain grazers such as cladocerans which can utilise pico- and nanoplanktonic size fractions (Carpenter 1988).

3. Grazers may show size-selective feeding and consume larger dividing cells ("production") rather than the smaller "standing stock" cells (Simek & Straskrabova 1992).

4. Protozoan DOM is partly in the form of dissolved *free* and *combined* amino acids (DFAA & DCAA respectively). Variations in the relative contributions of DFAA and ammonium release to the total flagellate nitrogen release is important in bacterial and phytoplankton ammonium uptake. This is because bacteria prefer DFAA to ammonium whilst phytoplankton prefer ammonium to nitrate, a relationship which affects competition for nutrients between these producer groups (Nagata & Kirchman 1992).

5. Generally, bacterial production and abundance are highest below the epilimnion during summer stratification, with grazing as the major bacterial loss factor. The importance of grazing is thus likely to depend on the importance of bacterial production compared with phytoplankton production (Sanders *et al* 1989).

6. Consumption of bacterivores by predators such as crustaceans is the likely but indirect link between bacterial production and the classic planktonic food web (Sanders *et al* 1989).

7. As mentioned above, summer conditions and the associated high zooplankton concentration mean that most primary production passes directly into the pelagic food web, reducing the bacterial role and favouring classical trophic links (Carpenter 1988).

Nutrient status also affects the linkage between the different elements of lake ecosystem functioning. Nutrient enrichment therefore has the following effects which are related to the processes likely to occur at Lake Naivasha as detailed above;

1. The microbial loop is less important.
2. Nutrient limitation is reduced and thus primary productivity increased.
3. The role of bacteria as a nutrient sink is reduced in importance.
4. There is still nutrient release by grazers, but this is less important.

1.7 Aims

Lake Naivasha is of international ecological and biological importance but is experiencing a number of potentially deleterious pressures. In summary these pressures consist of;

1. An expanding horticultural industry which is utilising increasing amounts of land surrounding the lake. Horticultural activity brings with it problems such as fertiliser and pesticide runoff, buffer vegetation clearance, increased local population due to the large *jua kali* workforce required, and irrigation water extraction. A large local workforce brings with it potential problems such as sewage disposal, overfishing and Papyrus clearance. Organisations such as the Lake Naivasha Growers' Group (LNGG) and LNRA have however begun to address such concerns in relation to horticulture, in order to produce more effective management plans.

2. The Ol-Karia geothermal power plant located approximately 5km south of the lake (Figure 1.2) contributes to Kenya's national electricity requirements, and is currently undergoing expansion with drilling in Hell's Gate National Park. This is approximately 10km from Elsamere, a conservation centre located on the southern shore of Oloidien Bay (Figure 2.1). This industry uses lake water for cooling, but does not return used water to the catchment, thus creating a net loss to the system.

3. As the main inflow to Lake Naivasha is the River Malewa, any threat to the level or quality of its water is of concern. There is already a dam on the River Turasha, a tributary of the Malewa, however previously shelved plans to dam the main river itself are locally believed to be under reconsideration. The LNGG and LNRA are opposed to this act and are likely to campaign against it, an action which previously helped prevent damming (LNRA pers. comm.). Ongoing work suggests that the main threats to Malewa water quality come from small-scale local activities such as *shamba* livestock-

watering (resulting in nutrient-rich faecal runoff) and clothes washing (resulting in detergent input). Such problems are magnified by increased erosion and the removal of fringing vegetation in *shamba*, especially those on steep river valley slopes during periods of heavy rainfall.

4. Within the lake itself, food webs are unbalanced due to the history of species introductions. This has no obvious impact on productivity processes although changes in predation upon zooplankton ultimately may affect productivity through changes in algalivory rates by grazers.

The aims of this study are as follows;

1. Through desk-based study of limnology, to develop a set of hypotheses regarding the factors controlling productivity in Lake Naivasha, to develop methodologies for the testing of these hypotheses, and to validate them in the field.

2. Through pilot study, to determine which hypotheses are most important and require further study to allow successful identification and investigation of productivity controls during fieldwork.

3. To describe, explain and quantify these productivity controls and their relative overall importance in Lake Naivasha, with extrapolation to shallow tropical freshwaters in general.

4. From this work, to understand the effect of system perturbations on overall lake productivity.

5. In parallel with work on nutrient sources and sinks being undertaken, to aid future environmental management of Lake Naivasha, including local monitoring programmes.

1.8 Hypotheses

From consideration of limnological theory as applied to shallow tropical lakes, and previous work undertaken at Lake Naivasha itself, a number of hypotheses were formulated;

1. Nitrogen is more limiting to primary production than phosphorus in Lake Naivasha.
2. Although different phytoplankton species utilise different nutrient forms, there is an overall algal preference for ammonium rather than nitrate as the latter requires more energy and use of the enzyme nitrate reductase if it is to be utilised.
3. Temporary stratification occurs diurnally due to surface heating and reduced wind strength, causing a diurnal cycle of environmental conditions. This is known to cause a very rapid anaerobic release of phosphorus from the lake sediment due to the reduction of iron in these sediments just prior to remixing by wind action and cooling.
4. Bicarbonate is the dominant inorganic carbon ion leading to alkaline conditions. The carbonate balance determines lake pH with eutrophic species tolerating higher pH levels and alkalinity will therefore partly determine species composition.
5. Phosphorus resupply from sediments is important in shallow lakes, and in eutrophic lakes faunal, water-column recycling is important. Lake Naivasha is both shallow *and* eutrophic, and therefore both these processes are important in facilitating resupply of phosphorus.
6. Seasonally stable ambient temperature means that the diurnal cycle is the scale primarily controlling succession, but there is a smaller longer-term component underlying this due to annual variations in rainfall and wind leading to changes in runoff, mixing, inflow and nutrient input.

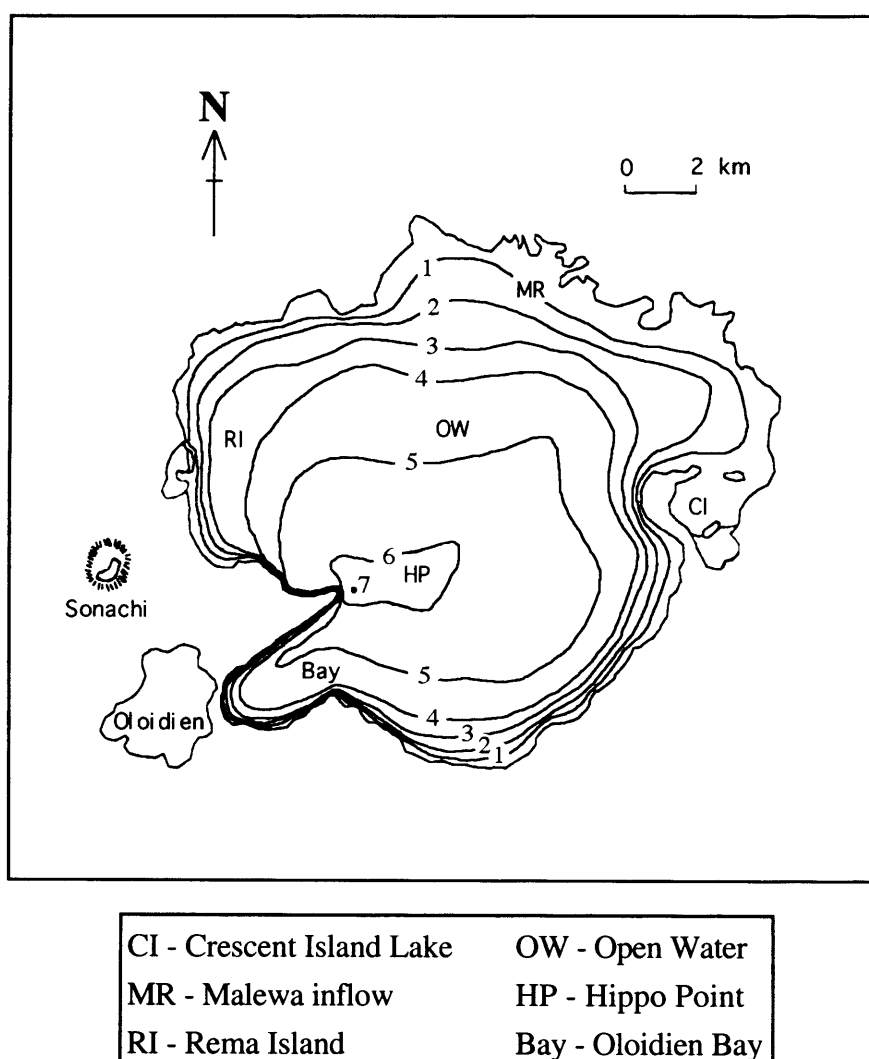
7. Reduced sunlight availability (due to turbidity and self-shading), high nutrient availability (due to eutrophication) and low sinking rate (due to the mixed water column) favour diatoms and maintain the algal community at an early successional stage.
8. As tropical waters appear to be in a state of permanent summer in many respects (Kilham & Kilham 1990), there is not necessarily any true seasonality even if succession is seen to occur. If there is long-term persistence of species and/or biomass, then *interannual* variations in climatic factors will be important.
9. The more numerous smaller phytoplankton with faster resource turnover have a more important contribution to lake productivity than the smaller number of larger, slower phytoplankton.
10. Productivity is primarily controlled by bottom-up factors such as nutrient levels with secondary effects due to top-down factors such as zooplankton grazing.
11. Light effects dominate other controls by determining the potential level of productivity. A light-adapted sample from a shallow depth should show poorer photosynthetic efficiency at a greater depth whilst a dark-adapted deeper sample should show greater photoinhibition near the surface.
12. The microbial loop is of reduced importance at Lake Naivasha.

2. Methods

2.1 Site description

The majority of sampling was performed on Lake Naivasha itself, although Lake Oloidien was sampled occasionally to provide a comparison with a developing soda lake in the same basin but under a very different chemical and hydrological regime. The inflowing rivers Malewa, Gilgil and Karati were also sampled to determine their contribution to the main lake's nutrient load. The Malewa is by far the larger of the three rivers and the Gilgil had often been diverted for agricultural purposes at the time of sampling.

Figure 2.1 Map of Lake Naivasha with sampling sites and 1991 depth contours (m).



The regular sampling sites on Lake Naivasha were chosen to provide a range of potential influences and resulting conditions and are as follows;

1. Crescent Island Lake - a deep (c. 20m) almost completely enclosed sub-basin.
2. Malewa River inflow - a shallow (c. 2m) turbid area where the River Malewa enters Lake Naivasha.
3. Rema Island - an inshore area about 4m deep away from any inflow.
4. Open Water - the central area of the lake which is well mixed with less shore effects than the rest of the lake. It is about 5m deep.
5. Hippo Point - A well-mixed inshore site, about 6m deep.
6. Oloidien Bay - well-mixed and approximately 3m deep with little agriculture or horticulture nearby, and opposite the main sediment input from the River Malewa.

These sites were chosen to provide a representative coverage of the different physical and chemical conditions found throughout the lake. Sites RI, OW, HP and Bay are collectively considered to form the 'Main lake' with results being agglomerated accordingly. The exact sampling sites are not very precise as buoys are generally difficult to locate and/or removed by fishermen (except for the fixed buoy at site CI). This is not expected to produce any significant error as there is relatively little horizontal variation. Transects used for investigation of river transport were taken approximately SW starting from site MR.

2.2 Fieldwork methods

1. Fieldwork was undertaken from February to May 1997, November 1997 to June 1998 and August 1998 to November 1998. Water sampling was carried out at known depths using a 1 litre messenger-activated Institute of Oceanographic Sciences (IOS) sampler. This was used to fill sample bottles, allowing overfilling to prevent trapping of air where this is important. Samples were not taken right to the bottom of the lake as sediments tend to be collected which would affect results, especially of nutrient analyses and oxygen levels.

2. A pilot study was used for familiarisation of the main algal forms present in Lake Naivasha and to give an idea of dominance within the phytoplankton assemblage at different sample sites. The pilot study was performed by taking samples and identifying the phytoplankton present using a selection of field guides and the help of colleagues. In order to investigate planktonic succession, all taxa remaining after 200 μ m screening were identified and counted along with grazing microzooplankton. Phyto- and zooplankton were identified to species where possible to allow investigation of species-specific environmental requirements for indicator purposes. Counts were made to genus level in most cases as identification of all individuals to species was often impossible and/or excessively time-consuming. Some taxa were grouped more broadly as the aim was a broad overview of planktonic succession rather than an in-depth study of community structure. Previous work, albeit on temperate grassland (Hubble 1996) and British rivers (Hawkes 1979), has shown that generic groupings can clarify otherwise complex community changes by reducing the number of groups requiring monitoring. This method also reduces the complexity due to species-specific environmental requirements, although the species forming a group must show broadly similar characteristics to avoid oversimplification and loss of useful successional information. Counting was undertaken using an eyepiece graticule and sedimentation chamber with a Zeiss Axiovert 100 inverted microscope (Zeiss, Germany). Cells were identified and counted along random transects covering 200 whole graticule areas. Cells were counted which were wholly within the area or touching the right or bottom edge. A multiplication factor then gave counts/ml depending on the volume of sample (usually 5ml) and magnification used (usually x400).

Flagellates, cyanobacteria and microzooplankton form three broad functional groups. The most important groups (those which form 10% or more of total cell numbers at any time) were separated from the results to identify any succession for a given sample site. Cyanobacteria were counted as numbers of colonies as the resolution of the available microscope (x400) made cellular counts impractical due to time and identification

constraints although a colony size:cell number calibration was developed separately. *Scenedesmus* was treated similarly as cell numbers were again predictable using a simple calibration. Some species were present in samples used to form the species list, but in such small numbers that they did not feature in counts. Counts were made of all identified taxa throughout fieldwork as any species could later prove important, giving a detailed picture of algal dominance and succession including structure and fluctuations of the overall algal community. Once succession was identified and described, the conditions which favour, or minimise losses to, the dominant taxa were determined.

Further information was derived by calculating Simpson diversity indices (D), and values of succession rate (day^{-1}) where;

$D = \sum P_i^2$ and P_i is the proportional numerical abundance of each species i (Simpson 1949).

Simpson's diversity scores were calculated for all samples counted and analyses performed between sites and depths to investigate both horizontal and vertical spatial variation in the algal community. To measure community change, estimates of succession rate were calculated (Jassby & Goldman 1974, Lewis 1976). These mathematical methods integrate changes in biomass or abundance over time through summation of such changes for each species as a proportion of the whole community. From this precept, Jassby & Goldman (1974) determined the succession rate (R_s) to be given by;

$$R_s = \sqrt{\sum (dc_i/dt)^2}$$

$$\text{where } c_i(t) = b_i(t) / \sqrt{\sum b_i(t)^2}$$

and $b_i(t)$ is the numerical abundance of species i at time t with n possible species.

Jassby-Goldman measurements do not include directional aspects of succession, therefore using the above equations but weighting all species equally gives the formula derived by Lewis (1976);

$$R_s = \frac{\sum i | \{b_i(t_1)/B(t_1)\} - \{b_i(t_2)/B(t_2)\} |}{(t_2 - t_1)}$$

where $b_i(t)$ is the abundance of species i at time t and $B(t)$ is the size of the community at time t .

Algae in surface film and benthic habitats were considered as well as those in the water-column. Samples of epilithic algae were taken by scraping stones taken from a known depth. The area scraped was measured so that counts could be converted to cell density per unit area. Benthic algae were sampled using a sediment corer and skimming approximately 1mm from the top of the core, again from a known depth. This provided estimates of cell density per unit area as the diameter of the circular core was 6.7cm, and hence the area covered was 35.26 cm². Calculating areal cell density assumes however that cells are only found on the surface of the sediment and not at any depth, despite the flocculent nature of the sediment-water interface. Before cores were skimmed, all particulate matter was therefore allowed to settle, including phytoplankton so that the 3-dimensional colloidal mix (which is in practise the lake bed) was sampled as a thin layer.

Sedimentation was quantified to determine its potential importance as an algal loss factor under a stable water column. This could occur through deepening of the lake or climatic change reducing wind velocity and/or regularity, especially during afternoon remixing events. To investigate sedimentation, mixed samples from main lake sites were placed in a 80cm high, 40cm diameter 100 litre barrel, with 1 litre subsamples taken at 25cm depth with an IOS sampler) for both algal counts and *in situ* productivity incubations immediately after experimental initiation (0 hours), and then after 4 and 8 hours.

Investigation of the tropical microbial loop was undertaken by determining proportions of bacteria, phytoplankton and protozoa from counts made using fluorescence microscopy (Hobbie *et al* 1977). Between 28 - 30/11/99, 1.5 litre samples were taken from the Main Lake, Crescent Island Lagoon and Lake Oloidien at 1m intervals from the surface to 5m depth. 2 ml aliquots were preserved in 4% formalin, 0.2 ml of 0.1 µg/ml DAPI stain (4,6-diamidino-2-phenylindole) added to each and left to settle for 5 minutes in the filtering apparatus. The aliquots were then drawn through pre-stained Nuclepore filters (0.2 µm pore size, 25 mm diameter) and the filters mounted on slides using immersion oil. 2 filters were produced for each sample except the 5m main Lake sample, for which only one was produced. Counts were made using a Zeiss III RS epifluorescence microscope with 360 nm excitation and 460 nm barrier filter.

3. A number of measurements were made using hand-held or bench-top meters. Temperature (°C) and dissolved oxygen (mg/l) were measured by electrode-probe using a YSI Model 50 oxygen meter (Yellow Springs Instrument Co., USA). Oxygen measurements were used to determine stratification and calculate stability as this is more clearly defined in terms of an oxycline than a thermocline. Conductivity was measured by probe using a portable Hach conductivity meter whilst measurement of pH was undertaken using a portable Hach pH meter/KCl electrode.

4. Transparency was determined by the extinction of a 20cm diameter Secchi disc. This is the depth where the disc vanishes and occurs when irradiance is approximately 15-20% of the incident level. From this, two calculations were made (Vollenweider 1974);

- a. The light extinction coefficient ($1.7/d$) and
- b. The euphotic depth ($2.35d$) where 1% incident energy remains,
where d was the extinction depth.

5. Light attenuation of red, green and blue bands of sunlight were investigated separately at all sample sites. This was done using a selenium photocell (with submersible detector and on-board reference cell) and meter (Lake Instrument Co. Ltd., Windermere) and red (RG2), blue (VG9) and green (BG12) glass Schott filters (Mainz, Germany) and opal diffusing filter. Profiles were taken during periods of equal (preferably zero) cloud cover and hence equal (preferably maximal) illumination. Black and white filters were used to help zero the meter during periods of high solar illumination. Timed Incoming Solar Radiation (ISR) data were available from the weather station for comparison with Secchi data when determining the absolute amounts of radiation penetrating the water column.

6. Paired light and dark incubation bottles (blackened with tape) were used with a 1m square wooden support frame and duplicate samples taken from the required depths using the IOS water sampler at 1 above. A YSI BOD (Biological Oxygen Demand) probe Model 5905 was used to measure dissolved O₂ after comparison with the traditional Winkler method (Mackereth *et al* 1989) to determine which was most suitable for use in later productivity experiments (section 2.6). Chlorophyll *a* measurements were also made in parallel with many incubations to produce a chlorophyll:productivity calibration so that if necessary, pigment concentrations could be used to estimate primary production. Incubations lasted approximately 2 to 3.5 hours.

Photosynthetic efficiency was calculated as a percentage of daily areal production per unit of daily solar energy. From Talling (1957) and Vollenweider (1974), the *in situ* 'photosynthesis-depth integral' (P_s) is calculated with units of mgO₂/m²;

$$P_s = P_{opt} / h_r \cdot L / e \cdot \ln (I_o' / 0.5 I_k)$$

where; P_{opt} / h_r = production at optimal irradiance per hour

L = day length in hours between sunrise and sunset

e = extinction coefficient of PAR

I_o' = Total subsurface irradiance

I_k = Light intensity at the intersect between the initial linear slope and the height of the saturation plateau of the photosynthesis - light curve (e.g. Figure 5.3.1). The $I_o' : I_k$ ratio is used to calculate P_s .

An estimate of maximum photosynthetic efficiency (f) in terms of energy utilisation is given by an equation which includes light saturation and allows for surface loss of radiation. This also provides a measure of the restriction on integral photosynthesis due to light saturation;

$$f = (I_k / I_o') \cdot \ln (I_o' / 0.5 I_k)$$

As I_k and I_o' are combined as a ratio in these calculations, values of I_k are given as a proportion of I_o' (i.e. I_o' is standardised to unity).

7. Other productivity work was also undertaken. The algal assemblage was split into 'small' (< 20 μ m), 'medium' (20 - 65 μ m) and 'large' (> 65 μ m) groupings using net filters of mesh size defined by filter size and algal functionality to determine the relative contributions to total productivity from larger, slower metabolising species and smaller, faster metabolising species. Functionally, phototrophs smaller than 20 μ m account for the majority of marine phytoplankton biomass and productivity (Sherr *et al* 1986). This filter size was chosen largely due to availability, with the assumption that small freshwater phototrophs had a similar function. Direct investigation of the controls on primary production was undertaken through experimental alteration of conditions known to affect them. This included grazing through dilution-exclusion methods (described in section 2.4.1), changes in the light regime and variation in the nutrient status of lakewater samples as detailed elsewhere. Stratified sampling was used to give a productivity profile showing the depth of maximum photosynthesis.

To investigate grazer preference for different prey types, 'with grazing' series (equivalent to post-grazing), samples were produced by screening at 200µm to remove zooplankton, whilst for 'without grazing' series (equivalent to pre-grazing) samples were filtered completely to also remove prey cells. The effect of grazing could thus be determined by taking the difference between the two conditions for a given dilution level. 'Production' and 'standing-stock' cells were distinguished visually by microscopy and counted for *Scenedesmus*, *Aulacoseira* and *Chlorella* as P-cells were the larger dividing forms. These genera are also numerous in the algal community and thus considered potentially important prey items.

Further work including serial nutrient enrichment was undertaken, with a much simplified initial experiment used to determine whether nitrogen is in fact the major limiting nutrient. At the Hippo Point site (which is representative of the main lake basin), productivity measurements were made in triplicate at a depth of 0.5m as this is where productivity was known to be approximately maximal from pilot productivity profiles. Nutrients were therefore most likely to become depleted and limiting at this depth. Productivity was measured with unenriched lakewater and with samples where either nitrogen or phosphorus concentration, or both, had been increased prior to incubation. The artificial concentrations used were 0.5 and 1.0 µmol/l which approximated to values found just above and below 0.5m in the water column where algal activity was reduced by either photoinhibition or light attenuation. In the full experimental design, major nutrients were investigated through serial enrichments with addition of 0 to 5µM SRP, and 0 to 10µM nitrogen fractions. Enrichments were 0, 0.1, 0.2, 0.5, 0.8, 1, 2, 5 and 10µM. More detailed low concentration series were also undertaken with 0.1µM increments from 0 to 0.5 µM. Minor nutrients were also investigated through serial enrichment, using Si(OH)₄, Na₂EDTA, MnCl₂ and FeSO₄.

8. Alkalinity titration was undertaken in the field using a Digital Titrator Model 16900-01 (Hach Company, Ames, USA). The associated Hach calculation was however

considered insufficiently accurate and the Freshwater Biological Association (FBA) calculation used in its place (Mackereth *et al* 1989).

9. Climatic factors were measured using an automatic weather station Model WS01 (Delta-T Devices Ltd., Cambridge, UK) which was installed at the Elsamere Field Study Centre. This incorporates a IBM-PC compatible data logger Model DL2e to allow long-term storage and periodic downloading of data. The station is equipped to measure the following parameters;

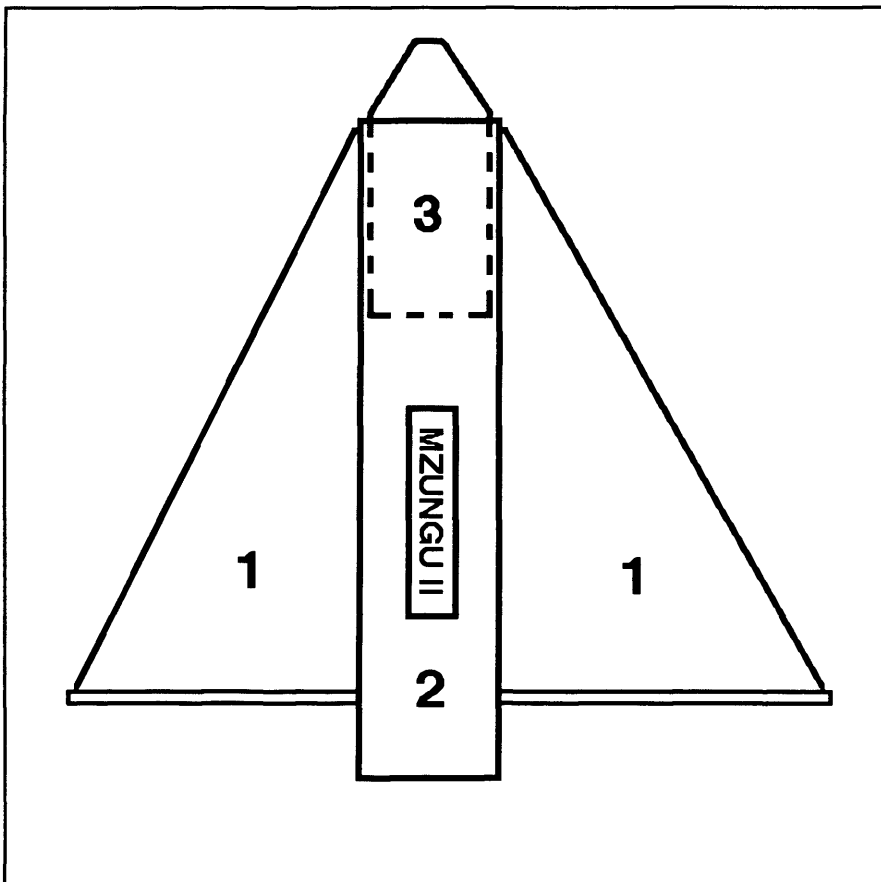
- a. Wind speed (m/s).
- b. Wind direction (degrees where 0° = northerly).
- c. Air temperature (°C).
- d. Soil temperature (°C).
- e. Relative humidity (%RH).
- f. Rainfall (mm).
- g. Incoming Solar Radiation (kW/m²).
- h. Atmospheric pressure (kPa)

As the rain gauge proved extremely unreliable due to blockage by dust, dead insects and algal growth on the gauge filter, rainfall data were acquired from other sources within the immediate vicinity of Lake Naivasha. Most of the rainfall data presented in section 4.1.4 were obtained from Sulmac Ltd. (a horticultural company) along with some data from daily reading of a simple post-mounted rain gauge, although it is recognised that significant errors may be associated with the design and location of such a device. Data for comparison prior to 1985 comes from the work of Ase (1987). Lake level and pan evaporation data were also obtained from Sulmac Ltd. Attempts were made to install a lake level gauge near Elsamere, but this was rapidly destroyed by either hippopotamus (*Hippopotamus amphibius*) trampling or large floating *C. papyrus* islands.

10. Two main methods were employed to investigate the transport of sediments and associated nutrients. Firstly, transects were sampled running from the mouth of the main inflow river, the Malewa (site MR, Figure 2.1) towards the centre of the lake with

vertical profiles also being taken at each sample point. Secondly, to investigate lake circulation (in conjunction with wind speed and directional data), an 80cm long, 1m wide drogue (Figure 2.2) was constructed which floats with its tip at the surface of the water and submerged sails. This permitted it to be transported by lake currents with minimal interference by wind which could otherwise move it in a different direction. To confirm that it could drift into the wind, the design was tested by observation in the lake. The movement of the drogue was followed by boat utilising visual landmarks around the lake to plot its location. The drogue was followed continuously for some sections and then taken by boat straight to the next drop-off point, although the direction of drift was checked periodically in these sections. This method was used because the currents were generally too slow to be able to cover the whole lake in the time available.

Figure 2.2 Lake drogue design (dimensions at point 10 above).



- 1. Cloth sails with vanes as weights
- 2. Plastic pipe
- 3. Plastic flotation bottle

2.3 Laboratory analyses

The analytical methods used were;

2.3.1 Phosphorus analyses

a. Total phosphorus was measured using an H₂SO₄-antimony and molybdate digestion method (Eisenreich *et al* 1975) but with a pressure cooker heated for 30 minutes replacing the furnace, and reagent/sample volumes were amended to fit the available glassware. This method also avoids dangerous acid digestion techniques.

b. Soluble reactive phosphate was measured using the malachite green technique (Baykov *et al* 1988) with the following adaptations;

i. During phosphate determination, the mixture was allowed to stand for 20 minutes instead of 10 as this allows more complete colour development.

ii. Absorbance was measured at 620 nm instead of 630 nm. This is laboratory convention as the absorbance band allows measurement at any point from 620 to 650 nm.

2.3.2 Nitrogen analyses

a. Nitrate nitrogen (NO₃-N) determination was undertaken by a revised technique developed from that of the Association of Official Agricultural Chemists (AOAC 1955) and is detailed fully in section 2.5.

b. Ammonium nitrogen (NH₄-N) was determined by the salicylate-cyanurate method of Havilah (1977).

c. Total dissolved inorganic nitrogen was determined by summation of nitrate and ammonium concentrations as nitrite concentrations were negligible. Total nitrogen (including the organic fraction) was converted into nitrate by heating with an alkaline

persulphate solution under pressure (Mackereth *et al* 1989). The concentration of nitrate was then determined using columns of Devarda's alloy as detailed above.

d. Nitrite nitrogen ($\text{NO}_2\text{-N}$) determination was undertaken by the diazotisation method as described in Mackereth *et al* (1989).

2.3.3 Other analyses

a. Chlorophyll *a* was measured by solvent extraction in either ethanol or methanol (depending on availability) followed by spectrophotometric evaluation of the sample. The ethanol extraction method (HMSO 1980) was generally used as alcohols are more effective extractants whilst ethanol provides a greater possibility of distinguishing between undegraded and degraded pigments. This is undertaken by pigment determination before and after acidification of the sample with hydrochloric acid.

b. Sediment concentration was measured by filtering a water sample of known volume onto a weighed filter paper and drying it to constant weight. The weight of sediment retained was then determined in g/l.

c. The following chemical constituents were periodically determined;

i. Concentrations of sodium (Na^+) and potassium (K^+) were measured with a gas-powered flame photometer using a gas supply in the nearby Geothermal Power laboratory.

ii. Calcium and magnesium levels were determined by compleximetric titration using EDTA (Mackereth *et al*, 1989).

iii. Sulphate (SO_4^{2-}), chloride (Cl^-) and fluoride (F^-) ions were determined by Hach spectrophotometry.

iv. Soluble reactive silicon (SiO_2) known as 'silicate' was determined by reduction to silicomolybdenum blues after Mackereth *et al* (1989).

2.4 Experimental Approach

In order to test the proposed hypotheses, the following approaches were considered;

1. Nitrogen and phosphorus limitation.

Nitrogen levels were measured as ammonium and nitrate ions, which together form the Total Dissolved Nitrogen (TDN) component, with TN being measured separately. Phosphorus levels were measured as SRP and TP. SRP includes PO_4^{3-} , HPO_4^{2-} and H_2PO_4^- ions, although the predominant form is pH-dependent, and is PO_4^{3-} in Lake Naivasha. Phytoplankton productivity was measured at existing nutrient levels to determine productivity under current resource conditions. Samples were then enriched with nitrogen and phosphorus separately (see page 51) under natural light conditions and productivity determined again to investigate whether there was a response to increased levels of nutrients. An increase in productivity with increased nutrient concentration shows this nutrient is limiting, although the N:P ratio ultimately determines which nutrient/s is/are potentially limiting. The absolute amounts of nutrient present control biomass.

2. Preference for ammonium over nitrate.

Ammonium and nitrate levels were measured as described above. If nitrogen is limiting, separate enrichment with these forms will produce different levels of productivity increase, with the preferred ion eliciting the larger response. If nitrogen is not limiting, a different approach is required with algal enrichment of a sample without artificial nutrient addition, from which ion depletion can be measured with the preferred ion again showing a greater response. The preferred ion should therefore show greater depletion.

3. Temporary stratification.

Dissolved oxygen (DO) levels were measured at different sites, times and depths in conjunction with light attenuation and temperature in order to detect the presence and

cause of any diurnal stratification. When stratification was detected, hypolimnetic phosphorus levels were measured throughout the stratification process along with oxygen levels to identify phosphorus release associated with deoxygenation in the lake sediments. Epilimnetic phosphorus levels were also measured to discount the possibility of substantial exchange across the thermocline. The major groupings of the algal assemblage were identified and enumerated using an inverted microscope and sedimentation chamber. The composition of the phytoplankton community was later related to physical conditions. Overall weather conditions were recorded including wind speed, wind direction and rainfall as these factors may also affect the mixing regime.

4. Light attenuation and photoinhibition.

Measurements of light attenuation in red, green and blue filtered wavelengths at different depths for a number of sites were compared with Secchi disc turbidity results and extinction coefficients. Photosynthetic efficiency was calculated as the photosynthetic rate per unit of Chl *a*. The effects of self-shading were investigated through algal dilution gradients and associated counts to estimate the loss of chlorophyll *a* efficiency. A reduction in photosynthetic efficiency with increasing algal numbers is thus due to overlapping and shading of Chl *a* units.

The magnitude of photoinhibition was determined from reduced photosynthetic rate and efficiency at shallow, light-saturated depths once any self-shading effects had been accounted for. Photoinhibition was investigated by incubating light-dark (LD) bottles at their original and other depths to show the effects of light-dark adaptation. Light-dark adaptation was investigated by incubating samples taken from 0 to 3m at the same range of depths. There would be a point where these two types of adaptation cancelled and productivity was equal between samples. This is termed the 'crossover depth' (D_x) and was estimated between samples. The depth of maximal photosynthesis was also derived at some distance below the surface.

5. Inorganic carbon.

As pH and alkalinity were known, the molarities of total CO₂, free CO₂, bicarbonate ions (HCO₃⁻) and carbonate ions (CO₃²⁻) were calculated, as well as hydroxide ions (OH⁻) although the latter was likely to be negligible. The fate of organic carbon products is too complex to investigate specifically, but will be involved in the functioning of the microbial loop.

6. Nutrient resupply and pools.

The grazing and nutrient dilution-deletion method used is described in section 2.4.1. The horizontal transfer of materials was also investigated by using a drogue and, where available, a portable Global Positioning System (GPS) to follow major lake currents (see section 2.3).

7. Ambient climatic conditions.

Both diurnal and longer-term temperature variations were measured and related to changes in algal composition from consideration of stratification and mixing regime using a YSI Model 50 temperature/O₂ probe. Temperature variations were related to productivity, along with other climatic variables such as rainfall, relative humidity, wind direction and wind speed (via a Delta-T Devices DL2e IBM-PC compatible data logger). The importance of different temporal scales involved and the effects of runoff, inflow and nutrient input where such data were available from co-workers, were then investigated. Variations in the mixing regime were also described and related to climate data. Short and longer-term trends or cycles were removed by subtraction to allow separate consideration.

8. Phytoplankton size and rate.

Phytoplankton were split into three size fractions by filtration and their contributions to overall productivity measured separately, with the size classes determined largely by availability of mesh sizes. Classes were functional where possible in terms of

contributions to overall productivity. The three fractions were W (whole water), A (< 20 µm) and B (< 65 µm). From these the contributions of fractions C (> 65 µm) and D (20 - 65 µm) could be calculated as $C = W - B$ and $D = B - A$. The separate contributions of classes A ('small'), D (medium') and C ('large') were then compared to determine which, if any, was the most important.

9. Control of primary productivity.

Bottom-up controls were investigated using the methods in 1, 2 & 6 above by consideration of nutrient levels and cycling. Zooplankton grazing was investigated by measuring productivity along a zooplankton dilution gradient, and also by parallel nutrient deletion to investigate both the effects of grazing alone and of nutrient pool contributions as described in 6 above. Zooplankton grazing was investigated primarily to determine whether top-down controls have a significant impact on productivity.

2.4.1 Methodology for evaluating grazer controls on productivity

Landry & Hassett (1982) and Landry *et al* (1995) estimated grazing impacts on algae through reduction of grazer numbers by 'diluting' whole water with the same water filtered clear of particulate matter with herbivorous zooplankton being those that pass a 200µm mesh. A dilution gradient can therefore be used to calculate grazing impact at any dilution, including algal growth without grazer activity. Dilution water is prepared by passing whole lake water through Whatman GF/C filters. Incubations were made with unfiltered fractions of 1.0 (whole water), 0.75, 0.5, 0.25, 0.2, 0.1 and 0 to form a grazing gradient, and were performed with and without enrichment. The standard dilution technique can only provide unbiased estimates of phytoplankton growth and microzooplankton grazing rates when the following assumptions are satisfied;

1. Growth of individual phytoplankton is not density-dependant.
2. The probability of a phytoplankton cell being consumed is density-dependant via the rate of encounters between prey and consumers i.e. encounter probability depends on

encounter radius, prey density and the swimming speeds of both predators and prey (Gerritsen 1980).

3. The change in phytoplankton density (P) over time (t) is adequately represented by the equation;

$$P_t = P_0 e^{(k-g)t}$$

where **k** and **g** are instantaneous coefficients of population growth and grazing mortality respectively. Where productivity measurements are taken instead of phytoplankton density, this logarithmic equation is however replaced by a linear relationship and therefore calculations of P, k & g are not required (Figure 5.1).

Given these assumptions it is important to consider the implications of diluting natural waters with filtered water of the same source. If nutrient levels do not change, neither should the instantaneous phytoplankton growth rate, whilst phytoplankton mortality should decline with dilution. Algal number (or chlorophyll *a* concentration) can also be used as a measure of dilution.

There is a problem when the water is capable of supporting much phytoplankton because there is then a non-linear relationship between grazer numbers and algal growth rate due to saturation of feeding. To solve this, Andersen *et al* (1991) combined dilution with nutrient enrichment which allowed differentiation of nutrients into three main pools, the contributions of which could be considered separately;

1. external (in water)
2. internal (in cells)
3. recycled (released by grazing)

Once incubations are complete, regression of phytoplankton growth rate (y) on grazer numbers measured as dilution in series (x) gives the maximum growth rate (y-intercept) and grazing impact (slope). Data requirements for these analyses are estimates of phytoplankton growth rates under experimental treatments (different nutrient and/or

grazing conditions) taken as chlorophyll *a* or in this case productivity. This produces linear plots without the need for logarithmic transformation.

When the natural phytoplankton are limited by one or more nutrients, omission of the limiting nutrient(s) in parallel dilution series will result in an altered relationship between net growth rate and dilution. Analysis of this relationship when the net growth rate at any dilution is corrected for grazing with the grazing coefficient factor obtained from the Landry & Hassett (1982) gradient allows differentiation of the contribution of the three sources of the limiting nutrient to growth. In dilutions, modified Jaworski's medium is added to supply trace metals (and vitamins if available), as well as silicate.

Deletion of a nutrient is accomplished by not adding that nutrient (Andersen *et al* 1991) and hence the treatments used were;

+ <i>N</i> + <i>P</i> receives;	10 μ M NH ₄ Cl	1 μ M KH ₂ PO ₄	5 μ M Si(OH) ₄
	1 μ M Na ₂ EDTA	0.1 μ M FeSO ₄	0.01 μ M MnCl ₂
- <i>N</i> receives;	all except NH ₄ Cl.		
- <i>P</i> receives;	all except KH ₂ PO ₄ .		

During actual incubations, bottles were tethered with their tops about 15cm below the surface, oriented vertically, for 2-4 hours i.e. the same arrangement used for standard productivity measurements. Vertical migration of zooplankton was not considered relevant to grazing experiments because it mainly occurs at sunset as a response to surface water, daytime fish predation (Wright *et al* 1980). Zooplankton therefore congregate near the surface at night when phytoplankton primary productivity is negligible. These accepted patterns of zooplankton vertical migration and fish predation were both observed regularly in Lake Naivasha. Low dissolved oxygen levels also elicit vertical migration (Meyers 1980) but this is not considered an important process in well-mixed and oxygenated lakes such as Naivasha. These results can thus be considered alongside top-down grazing control as investigated in section 5.1, whilst algal number can also be used as a measure of dilution, allowing algae to be applied as ecological indicators as detailed in Chapter 3.

2.5 A revised method for nitrate analysis

This method was developed from that of the AOAC (1955) and uses a column of Devarda's Alloy and inert fused silica anti-bumping granules which reduces nitrate to ammonium. Traditionally, the analysis of low concentrations of nitrate nitrogen ($\text{NO}_3\text{-N}$) in natural waters has required reduction by cadmium as with the spongy cadmium method detailed in Mackereth *et al* (1989) and the cadmium-copper method described in Wetzel & Likens (1991). Cadmium-based methods are however potentially problematic for a number of reasons;

1. Cadmium is toxic and bioaccumulative in both humans and the environment and there are no adequate disposal facilities in Kenya.
2. The production of spongy cadmium using cadmium sulphate was also deemed unsatisfactory due to the lack of safety equipment such as fume cupboards in the available laboratory facilities.
3. The reaction using cadmium also has an unstable end-point and is prone to timing errors.
4. High quality analytical cadmium or cadmium sulphate were not easily available in Kenya, nor could they be transported by air due to toxicity and the resulting prohibitively expensive freight-packaging regulations.

The use of Devarda's Alloy is safer as the reagents are less hazardous, and the end-point of the reaction is stable and less prone to timing errors (Wetzel & Likens 1991) than the cadmium-based method. Devarda's Alloy is also easier to purchase and transport when required for overseas use. It is generally used as a reducing reagent in nitrate analyses which are less sensitive than cadmium-based methods. Sensitivity was

increased by mixing the alloy with inert fused alumina anti-bumping granules to form a matrix in a custom-built glass column. This maintains the high surface area of the finely divided alloy whilst allowing samples to flow over the reagent long enough for nitrate to be fully reduced to ammonium in a 1:1 ratio, thus increasing sensitivity. The procedure used was as follows;

A glass column, pre-washed with 10% nitric acid, was filled to a height of 15cm with an approximately 4:1 to 5:1 mixture by volume of anti-bumping granules and Devarda's Alloy (Figure 2.3). Excess Devarda's Alloy was avoided as it tended to fuse and block the flow of samples once the column had dried between uses. Too little alloy however prevented the column from efficiently reducing all the nitrate present. A low-lead glass wool plug was inserted in the tapered section of the column to prevent the escape of alloy powder or blockage by small granules. The small amount of alloy which occasionally flowed from the column simply settled out in the sample and was left behind when pipetting into sample tubes and thus did not affect spectrophotometry.

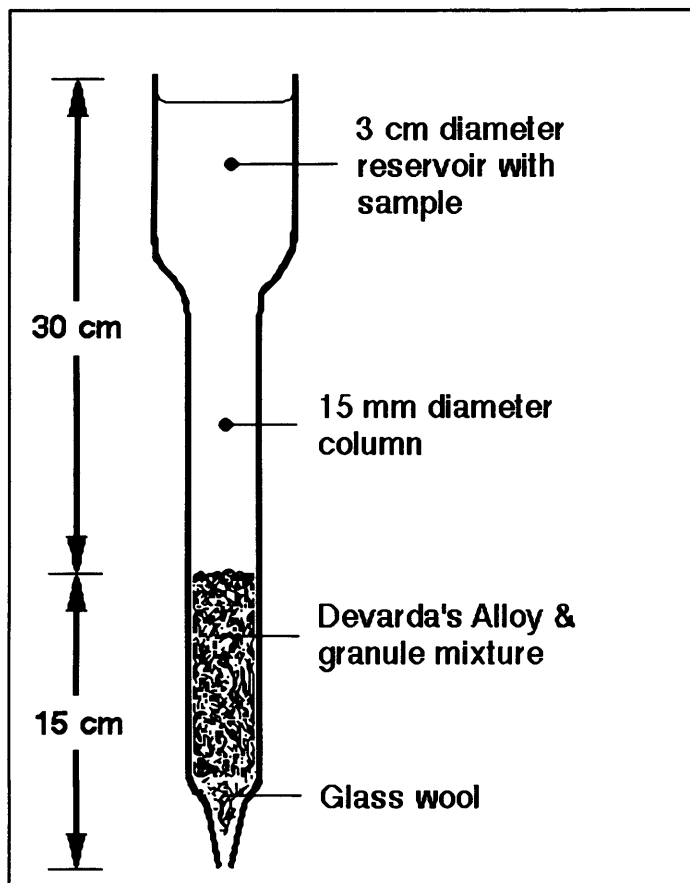
Samples or standards were added to the reservoir and allowed to drain through into a measuring cylinder, the first 10ml collected being discarded to prevent contamination from previous samples. The remainder was analysed in a Hach DR/2000 spectrophotometer using the salicylate-cyanurate method for ammonium analysis of Havilah *et al* (1977) as ammonium (unlike nitrate) can be analysed directly by colorimetry. Subtracting the background levels of ammonium, obtained by analysis of untreated samples, from the results gave the concentration of nitrate.

Subtracting the background levels of ammonium (obtained by analysis of untreated samples) from the results gives the concentration of nitrate as the reaction converts nitrate to ammonium with a 1:1 ratio. There are two main maintenance issues involved with this technique as it is still undergoing development and therefore needs care to prevent avoidable errors in nitrate determination;

1. The system is flushed through with 50ml deionised water both before use and before a period of storage. During storage the open ends of the column are covered with Nescofilm™ to prevent contaminants or organisms entering the system.

2. Periodic emptying, remixing and refilling of the columns are also undertaken as the alloy powder tends to be washed downwards and solidify, blocking the system although it does adhere to granules effectively. If the alloy-granule matrix does solidify, it also adheres to the glass, and a new column is constructed.

Figure 2.3 Nitrate reduction column using Devarda's alloy.



The methods were run in parallel in Leicester to determine the effectiveness and accuracy of the novel Devarda's alloy column in comparison with the accepted cadmium-based methodology. Calibration curves for the two methods are shown in Figures 2.4 & 2.5, and indicate that both methods produce precise calibrations when

undertaken carefully. The tap water samples gave mean values of 0.011 and 0.010 mM $\text{NO}_3\text{-N}$ for the Devarda's alloy and spongy cadmium methods respectively. Applying a 2-tailed paired-sample t-test gave a value of $p = 0.688$. Similarly, the pond water samples gave mean values of 0.111 and 0.113 mM $\text{NO}_3\text{-N}$ for the Devarda's alloy and spongy cadmium methods respectively and a value of $p = 0.495$. These results indicate no significant difference between the results obtained by the two methods.

Figure 2.4 Calibration for the spongy cadmium method of nitrate analysis.

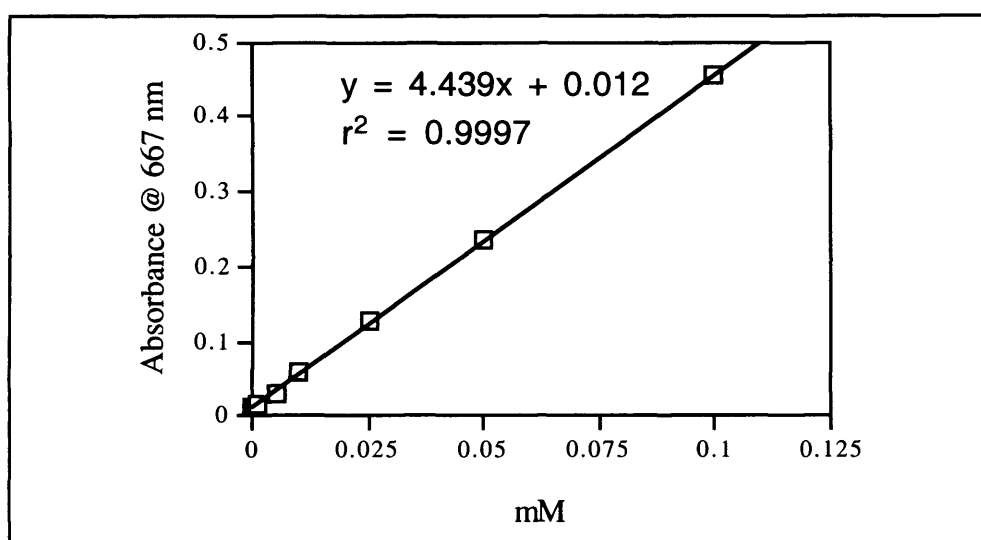
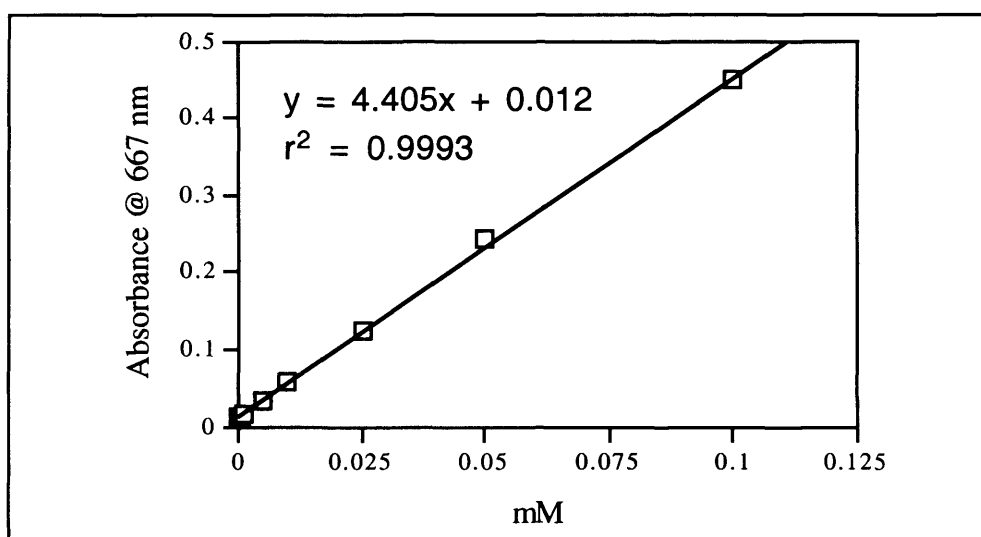
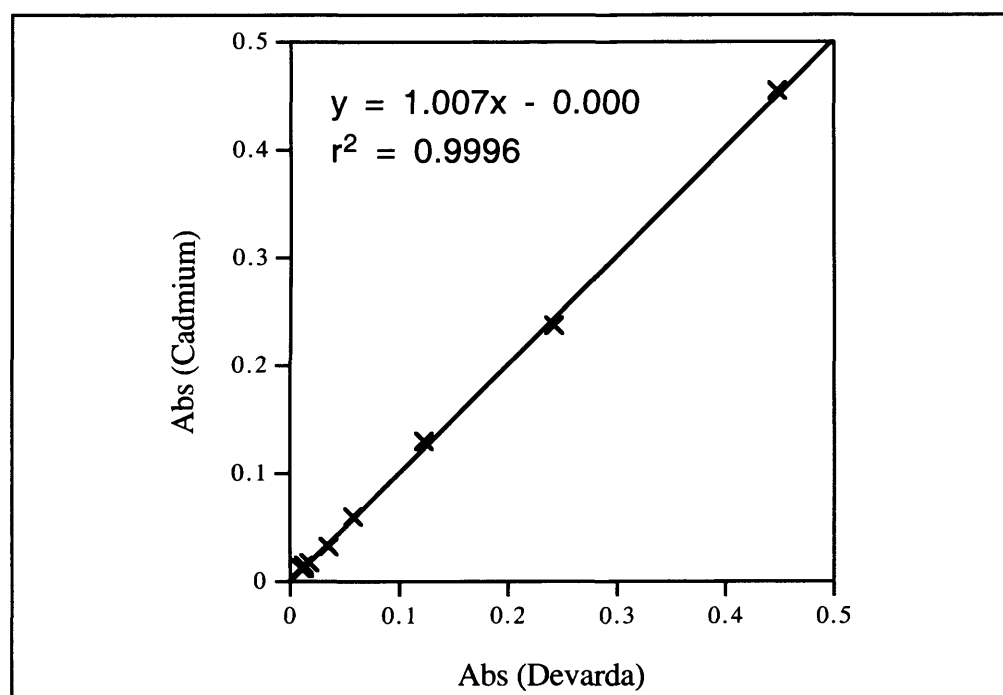


Figure 2.5 Calibration for the Devarda's alloy method of nitrate analysis.



Comparing these methods further using analysis of variance (ANOVA) for the calibration series data, a value of $p = 0.704$ was obtained, indicating no significant difference between the two methods. Figure 2.6 shows regression of these methods, with an r^2 value of 0.9996 illustrating the similarity in results. The Devarda's alloy method was therefore considered suitable for nitrate analysis at low concentrations as the technical problems encountered were minor.

Figure 2.6 Regression of absorbance values from Devarda's Alloy and spongy cadmium methods of nitrate analysis.



2.6 Comparison of titration and electron-probe methods

2.6.1 Introduction to methods

Traditionally, the Winkler titration (Mackereth *et al* 1989) is employed for accurate dissolved oxygen determination when measuring aquatic primary production using *in situ* light and dark bottles. As noted by Wetzel & Likens (1991), previous electrode-probes, although much less time-consuming than the titration, have suffered from difficulties in maintaining the required high accuracy (better than $\pm 3\%$). To investigate

whether advances in probe design have solved accuracy problems, the YSI Model 5905 BOD probe was compared with titration to show whether a new electrode-probe could provide suitable accuracy and precision. For the Winkler titration, the oxygen concentration in a sample = $(8000n/V)v$ in mg/l, where v = the volume of thiosulphate of molarity n used in the titration itself.

For both methods, productivity in terms of gross photosynthesis (mgC/m³/hr) can be calculated as;

$$\text{Gross Photosynthesis} = \{(O_2LB - O_2DB) * 1000 * 0.375\} / 1.2t$$

where O_2LB and O_2DB are light and dark bottle dissolved oxygen concentrations (mg/l) respectively and $1.2t$ is the incubation time (t hours) multiplied by the photosynthetic quotient (ratio of O_2 molecules liberated to CO_2 molecules fixed) for an active photosynthetic system (Kirk 1994) such as that found in the tropics. Samples 1-5 are from surface water, samples 6-10 are from a depth of 2m. Incubation was *in situ* for 1.5 hours at an initial temperature of 21.0°C. The volume of sample titrated (V) was 50 ml with thiosulphate of molarity (n) 0.0126M.

2.6.2 Results from comparison of methods

Comparing probe and Winkler-derived results using 2-tailed t-tests ($df = 4$, $t_{tab} = 2.776$ for $p = 0.05$), there is no significant difference between the results obtained from these contrasting methods ($t_{calc} = 0.946$ for surface water, $t_{calc} = 0.046$ for 2m depth). Table 2.1 shows results for the comparison between probe (P) and Winkler (W) methods.

As well as being much faster (a reading can be taken within 30 seconds), the BOD probe produces lower standard deviation. This stems from Winkler precision being limited by the accuracy of burette reading whilst probe precision is limited by the accuracy of meter reading. A limit of ± 0.05 ml in burette reading equates to ± 0.1 mg/l O_2 , whilst the limit for meter reading is only ± 0.05 mg/l O_2 . The probe can also be used *in situ*, dispensing with the need for sample preservation and storage. Finally, it is

relatively free from errors inherent in the titration such as poor sample preservation and/or storage, iodine loss by volatilisation, optical and iodine absorption by particulate material, organic matter or reducing agents, CO₂ liberation when acidifying alkaline waters, and accuracy of end-point determination (Carpenter 1965).

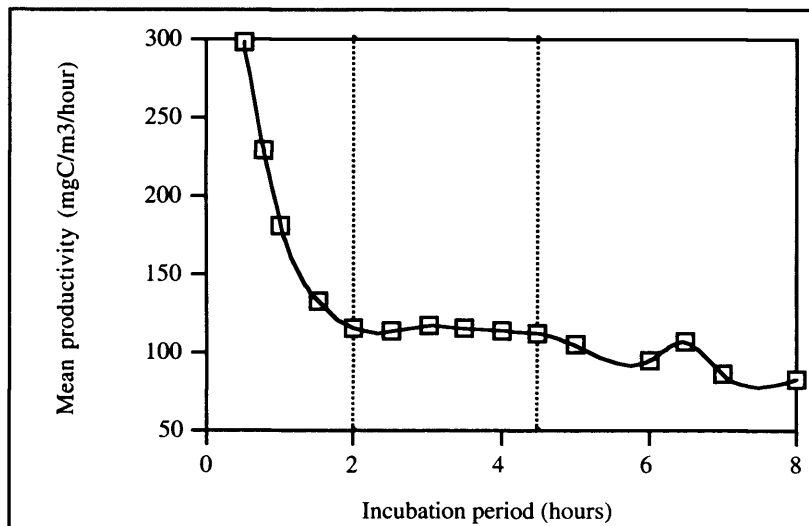
Table 2.1 Comparison of probe and Winkler methods for productivity measurement.

Sample number	L-D DO ₂ difference	Productivity (mgC/m ³ /hr)
P1	0.75	156.25
P2	0.80	166.67
P3	0.70	145.83
P4	0.75	156.25
P5	0.75	156.25
Mean	N/A	156.25
Standard Error	N/A	3.30
W1	0.7056	147.00
W2	0.8064	168.00
W3	0.7056	147.00
W4	0.7056	147.00
W5	0.7056	147.00
Mean	N/A	151.20
Standard Error	N/A	4.20
P6	0.25	41.67
P7	0.20	52.08
P8	0.30	62.50
P9	0.30	62.50
P10	0.25	52.08
Mean	N/A	54.17
Standard Error	N/A	3.90
W6	0.2016	42.00
W7	0.3024	63.00
W8	0.4032	84.00
W9	0.2016	42.00
W10	0.2016	42.00
Mean	N/A	54.60
Standard Error	N/A	8.40

2.6.3 Stability of productivity measurements

In productivity experiments, short incubations prevent the Warburg Effect which reduces the productivity measured over longer time periods (Round 1981). Incubations were therefore run over a variety of time periods in order to check for non-linear responses, and hence find a viable range of incubation lengths. This was done three times, once before and twice during fieldwork. Figure 2.7 shows linear responses with incubation lengths of approximately 2 to 4.5 hours as indicated by broken lines. Most productivity experiments used a 2.5 to 3.5 hour incubation, which parallels other work at Naivasha (e.g. Kitaka 1991) which also reported irregular results with longer or shorter incubations. As noted by Vollenweider (1974), shorter incubations tended to be inaccurate, in this case overestimating productivity above natural levels, an error partly due to the limited resolution of either method used (burette or meter reading) and time occupied in manipulations as the period exposed to air becomes significant. Longer incubations tended to show the Warburg effect as well as more variable results.

Figure 2.7 Stability of productivity measurements during incubations.



Longer incubations were therefore avoided for the following reasons;

1. High levels of irradiance in tropical regions may cause excessive photoinhibition and thus reduced productivity measurements, especially in incubation bottles near the surface of the water.

2. Incubations could not be observed full-time, exposing equipment to interference from humans, floating plants and animals such as hippopotamus.
3. Short incubations could take place during daylight when climatic conditions were stable, before late afternoon turbulence due to increased wind speed, and the reduction in insolation due to cloud formation.

2.7 Limitations of methods used at Elsamere

Climate data were more fragmented than expected due to weather station logistical problems, human interference with the station, irregular downloading of data outside fieldwork sessions and a non-functional rain gauge. Human interference with other equipment such as productivity incubations meant that such experiments could not be left unattended as local fishermen would steal the floats, leaving the rest of the apparatus, including expensive Pyrex bottles, at the bottom of the lake. Most experiments were therefore performed relatively near to Elsamere which also alleviated the problems of boat and vehicle availability. This means that the sites in Oloidien Bay and off Hippo Point were used much more often than other sites. This is not considered a problem as physico-chemical results show they are representative of the main lake, and experiments were able to be carried out at all sites during fieldwork. Equipment was mostly old and in need of maintenance or repair, and breakdowns meant that some parameters could not always be measured. Problems keeping materials clean and free of dust and invading insect life are believed to be a major factor contributing to periodic failures in chemical analyses. This was a particular concern when high-quality deionised water was required as the still was not always reliable, and itself suffered from ant infestation. Investigation of faunal recycling using the proportion of nutrients found in zooplankton in terms of faunal phosphorus content (by digestion) and possibly C:H:N analysis was considered but these facilities were unavailable in Naivasha.

Some other considerations are fundamental to the work being undertaken. For instance, details of nutrient status are required, however nutrients are in some ways poor

variables to sample as they are non-conservative being heavily depleted when limiting (although the limiting nutrients are those about which most information is required). This means that enrichment increases maximum but not minimum nutrient levels, potentially increasing the amplitude of any fluctuations and obscuring some minima by causing productivity (or biomass) peaks to merge. As a lake system becomes more eutrophic, more samples are also needed to define a maximum or mean as estimates of variables such as algal numbers based on single measurements become less secure. Where possible, it is therefore particularly important to perform replicates of any measurements taken in Naivasha.

3. Plankton communities and ecology

Lake Naivasha is now considered moderately eutrophic (Harper *et al* 1993), and ongoing eutrophication will affect the balance of algal species as well as increasing overall production. Aside from visual changes such as increased turbidity, the work of Melack (1979) gives a primary productivity value of 77.5 mgC/m³/hr showing that productivity has increased by approximately 50% (with higher peaks) since the 1970s. As this process is still occurring, it is important to consider whether the algal community is in a state of flux.

If so, and eutrophication progresses, populations are likely to peak more often and/or at different times changing any underlying successional patterns with the possible merging of growth peaks allowing greater dominance by a single species. If the system described by Lewis (1978) is followed, eutrophication would therefore favour succession by green algae in place of the current diatom-cryptomonad dominance.

3.1 Results

In Lake Naivasha, the diatom genus *Aulacoseira*, especially the species *A. italica* has been most dominant throughout this study. The seasonality as determined by bimodal rains has not been seen during this period (1996-1999) due to unusual weather patterns leading to droughts, and the floods attributed to the El Niño phenomenon. Complex successional changes have been observed in the algal assemblage, but they do not appear to be regular or easily explained by perceived changes in environmental factors.

Counts show a succession of dominant groups in Lake Naivasha beginning with *Scenedesmus* in December 1997, and changing on an approximately monthly basis to *Aulacoseira*, flagellates, cyanobacteria and finally *Ceratium* by May 1998 before returning to *Aulacoseira* dominance. The algal community and its succession is

described in detail but is inherently difficult to explain due to the complex interplay of factors affecting the wide range of species present. The change in dominant species is clearly illustrated and is linked to grazer preference in that the most preferred prey taxon tested, *Aulacoseira*, is also often the dominant taxon in the lake, and thus responsible for a greater proportion of primary production than any other group identified in the extensive counts. This may explain why grazing exerts a noticeable top-down control in a moderately eutrophic system where such a control might be expected to be of minor importance. The effect however is much outweighed by nutrient limitation and is much smaller than that seen in less productive systems (Sanders *et al* 1989).

Investigation of horizontal and vertical spatial variation in the algal community using diversity scores can be considered in conjunction with spatial variations in nutrient levels, physico-chemical conditions and productivity. Considering depths 0m, 1m, 3m and 7m at site CI (as the only site showing regular stratification) using t-tests and ANOVA, the most significant variation was between 0m and 7m, indicating that there is active (through buoyancy regulation) and/or passive (through mixing) algal movement towards the surface to avoid sedimentation which is shown to be an important loss-factor in a stable water-column. Without this resuspension, all species would sink and the same community would be found at depth although productivity would be effectively zero due to light attenuation and there would thus be fewer living cells. Routine monitoring in lake Naivasha has shown that mixing always occurs down to approximately 3m at site CI, although there is less difference between 1m or 3m samples and deeper water suggesting that algae stay in the near-surface water between 0m and 1m depth. This is borne out by the highest level of productivity being found at approximately 0.25 - 0.5m where the combination of photoinhibition and light attenuation is at its minimum. There is more variation over time due to succession ($p \approx 0$) than spatially due to depth ($p = 0.018$) or site ($p = 0.284$), although there are differences between diversity values at all depths.

3.1.1 Algae of Lake Naivasha

There are a wide range of bacterial & algal species in Lake Naivasha, ranging from the cyanobacteria to the green Chlorophyta and the dominant group, the Bacillariophyta, more commonly known as diatoms. Algae, as well as being the main primary producers within the lake, are sensitive indicators of environmental conditions; therefore the presence (or absence) of certain species can provide useful information about the waters in which they are found. For this reason, a list of the 170 identified species (and 8 identified to genus only) is presented in Appendix 2, but more importantly details of the environmental requirements of individual species are included for use when investigating water quality. Comparison can be made with the 143 taxa identified by Kalff & Watson (1986) during 1979-80. No relationship was found between species abundance and algal biomass, the latter being used as a measure of lake trophy in this earlier study. 43 species are common to both studies, although it is important to note that species richness may be seriously underestimated even for large samples of a speciose community (Lande 1996). This is because in natural assemblages, increasing competition amongst individuals in a community can lead to competitive exclusion. Thus as the density of individuals increases, richness does not increase with sample size as much as expected (Goldberg & Esterbrook 1998). This may be seen for dense *Ceratium* populations in Lake Naivasha. However, the main direction of this study is productivity control and hence such considerations, although interesting, are only of secondary importance.

Currently, Lake Naivasha has a moderate electrolyte content (approximately 250 $\mu\text{S}/\text{cm}$), and is considered moderately eutrophic. The Naivasha sewage treatment works has tertiary oxidising ponds and produces effluent which does not reach the lake (Harper *et al* 1993) which consequently does not suffer from serious organic waste pollution. Algal taxonomy undergoes changes and the precise system used may vary between authors, therefore identified species are merely grouped into phyla and orders.

Most sampling was from the water column as nutrient analysis was being undertaken concurrently. Planktonic forms were therefore collected more often, although sufficient benthic and epiphytic samples were taken to provide a comprehensive representation of lake species, whilst some individuals were presumably transported by the River Malewa, and thus some rarely-encountered species may not normally be associated with the conditions where they were sampled. The collection of a comprehensive set of samples was aided by many benthic or epiphytic species simply being attached forms of planktonic species. Due to their accepted use as ecological and environmental indicators (Lobo *et al* 1995), diatoms form the focus when considering algae in such a role. Cox (1996) gives details of species' distribution and environmental requirements.

Firstly, *Achnanthes* (now largely reclassified as *Achnantheidium*) are generally epiphytic and common in most waters. For instance, *A. exigua* is widespread, particularly in slightly alkaline waters of moderate to high electrolyte content. *A. minutissima* is similarly widespread and common, comprising a number of ecological races and hence being found in waters with a wide range of quality, although the species is sensitive to waste-water or more than moderate pollution levels. The filamentous colonial *Aulacoseira*, the most dominant genus in Lake Naivasha, is represented by 3 species, *A. ambigua*, *A. granulata* and the most common, *A. italica*. These are all associated with eutrophic waters and are generally considered both widespread and planktonic, although many species are planktonic in the tropics but benthic in temperate zones. Conversely, *Diatomella* is an unattached benthic genus, and probably consists of a single species, preferring alpine areas although any relatively upland waters may be suitable as Lake Naivasha is situated at an altitude of 1890m. The genus *Cyclotella* is considered widespread, usually planktonic and often profuse in lakes although due to taxonomic confusion and disagreement about the species' ecology, their use as environmental indicators must be treated with caution. *C. meneghiniana* is however associated with the littoral regions of eutrophic lakes whilst *C. stelligera* is common and widespread throughout freshwaters. The superficially similar *Stephanodiscus*

neoastraea is also generally planktonic in nutrient-rich lakes. *Cocconeis placentula* is another variable species, and is both widespread and common, epiphytic in both still and flowing mesotrophic to eutrophic waters. It was only identified occasionally in Lake Naivasha possibly due to the scarcity of submerged macrophytes, although it can also be found on wood and stone substrata. Similarly, *Diatoma ehrenbergii* occurs in a wide range of freshwaters whilst *D. tenuis* can be either planktonic or epiphytic in moderate to raised electrolyte conditions. Both *Fragilaria capucina* and *Eunotia monodon* were rarely found; this may be due to their requirements for oligotrophic (or weakly mesotrophic) moderately acid (or circumneutral) conditions with low to moderate electrolyte levels.

Following the water level decline between 1980 and 1987, and subsequent inundation of cultivated land (Harper *et al* 1993), this set of conditions is no longer found in Lake Naivasha. The low populations may be merely a relict, although *F. capucina* is known to exist as a number of ecological races. The lack of historical data regarding population levels unfortunately makes it impossible to investigate this area more fully without undertaking palaeobotanical counts. Conversely, several *Synedra* species were identified, most of which tolerate a range of environmental conditions. For example *S. acus* is generally epiphytic in mesotrophic to eutrophic waters and *S. berolinensis* is planktonic in circumneutral standing waters of moderate electrolyte content. The more generalist *S. capitata* is tolerant of slight pollution in oligotrophic to eutrophic waters with higher electrolyte levels, whilst *S. ulna* is widespread and morphologically variable in mesotrophic or eutrophic conditions.

The order Naviculales produced the greatest number of diatom species, partly due to the numerous *Navicula* and *Nitzschia* species present and thus provides a useful group for use as indicators. *Amphora ovalis*, *Cymatopleura solea*, *Encyonema prostratum*, *Caloneis amphisbaena* and *Epithemia turgida* are generally found in waters with moderate to high nutrient and electrolyte levels but are otherwise widespread. The latter species is also sometimes associated with cyanobacteria, although none of the resulting

gelatinous masses were found. Of the Naviculales species identified, *Encyonema minutum* requires oligotrophic, moderate electrolyte conditions. The *Gomphonema* species identified also prove to be useful indicators due to having well-documented levels of pollution tolerance. *G. acuminatum* although not numerous in Lake Naivasha is widespread in circumneutral to slightly alkaline waters as found there, but is sensitive to pollution greater than BOD = 4 & O₂ deficit = 30%, as is the most commonly identified member of this genus, *G. truncatum*, also widespread and common in electrolyte-rich waters. Despite having different nutrient requirements, both *G. augur* and *G. olivaceum* tolerate pollution levels up to BOD = 7 & O₂ deficit = 50%.

The genus *Navicula* provides species with a wide range of environmental requirements although many are quite generalised. For instance *N. schoenfeldii*, *N. trivialis*, *N. lanceolata* and *N. capitata* are widespread throughout a broad ecological spectrum with *N. capitata* tolerant of pollution levels up to BOD = 13 & O₂ deficit = 75%, whereas *N. radiosa* tolerates pollution levels only up to BOD = 4 & O₂ deficit = 30% (and has no clear pH or conductivity range). *N. cryptocephala*, although associated with more oligotrophic electrolyte-poor waters, is found quite commonly in Lake Naivasha and is thus considered to be the form *N. c. exilis* as it is found in moderate to high electrolyte conditions. The genus *Nitzschia* contains similarly generalist species, although *N. fonticola* (moderately frequent in Lake Naivasha) is thus particularly useful as an indicator of clean water, only tolerating pollution up to BOD = 4 & O₂ deficit = 30%, and usually being found where BOD < 2 & O₂ deficit < 15%, with moderate to high electrolyte content. *N. acicularis* and the related *Tryblionella apiculata* (previously known as *Nitzschia constricta*) are however tolerant of pollution up to BOD = 13 & O₂ deficit = 75%, being widespread and planktonic or epipelagic in eutrophic, moderate to highly electrolytic conditions. Other pinnate species are also found covering a wide range of habitat requirements. *Pinnularia maior* and *P. viridis* for instance are associated with low electrolyte and nutrient conditions not found in Lake Naivasha. *Rhopalodia gibba* and *Surirella linearis* are widespread, occurring commonly in moderate to high

electrolytic waters whilst *Stauroneis anceps* is a common generalist with a variety of ecological forms. The lake however supports only low numbers of all these species, despite the more favourable conditions for *R. gibba* and *S. linearis*.

Non-diatom species are presumably equally viable indicators but little species-specific information is available, however some generic environmental requirements are well understood if somewhat generalised. For instance, within the order Desmidiaceae (the desmids), the genera *Cosmarium*, *Stauroidesmus*, *Staurastrum* and *Gonatozygon* are all associated with lake-edge macrophytes but can also survive well as planktonic forms. *Closterium* is a widespread group, often being the only desmid genus in an algal assemblage, with some species able to tolerate highly polluted or eutrophic waters over a range of pH conditions. Other groups are described in similarly generalistic terms.

As the relationships between diatom species and their aquatic environment are complex, a simplified listing of species which have easily defined environmental requirements is given in Appendix 1 with species divided into a number of broad ecological groups. From this it can be seen that the majority of species are widespread generalists or are associated with mesotrophic to eutrophic waters as found in Lake Naivasha. Similarly most are associated with moderate electrolyte levels and circumneutral to slightly alkaline conditions. This supports the identification and indicates the ecological importance of chemical conditions in the water column.

3.1.2 Colonial forms

Some phytoplankton are colonial, therefore counts of colony numbers may be misleading if cell numbers are variable. Counting all cells in all colonies sampled is extremely time-consuming and therefore mean cell numbers per colony or colony size:cell number calibrations can be developed. This work was undertaken with colonies of *Aulacoseira*, *Microcystis* and *Scenedesmus* all of which were encountered commonly. Despite the difficulties involved in counting small cells, a close relationship

is shown between cell number and colony diameter. Figure 3.1a shows this close power relationship between the coenobial *Microcystis* colony diameter and the number of cells. The apparent packing density of cells reduces with colony size. Figure 3.1b shows the similarly close power relationship between colony diameter and the density of cells within the colony. Correlating these results gives Pearson correlation (C_p) = 0.927 ($p < 0.001$, $df = 113$) for colony diameter and cell number, and $C_p = -0.617$ ($p < 0.001$, $df = 113$) for colony diameter and cell packing density. This shows that larger colonies, whilst having more cells, develop with cells less densely packed. This may help to prevent self-shading within the colony and therefore is either a genuine trend in *Microcystis*, or could be due to cells being obscured by others and remaining uncounted. *Scenedesmus* were simpler to count as cells and a sample of 100 colonies were enumerated, giving a mean value of 6.28 cells per colony. 4- and 8-cell colonies were the most common although unicells were difficult to identify accurately. Figure 3.2 shows the full range of colonies sampled.

Figure 3.1 Regression of *Microcystis* cell number and colony size (a) / cell packing density and volume (b).

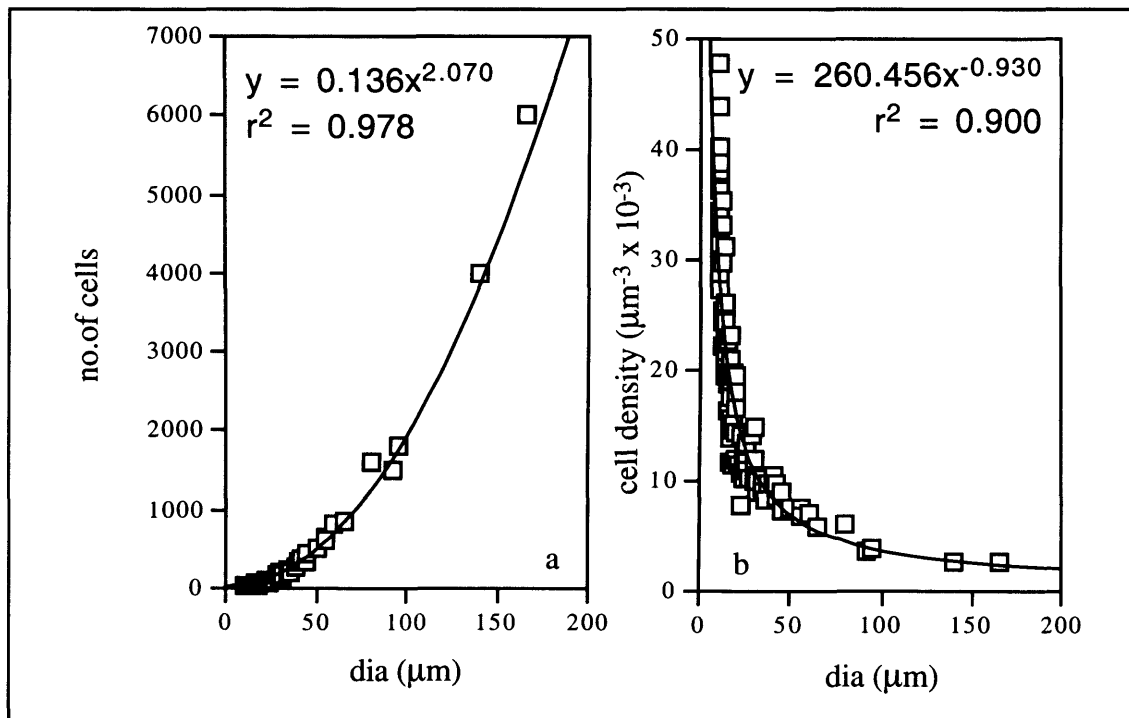
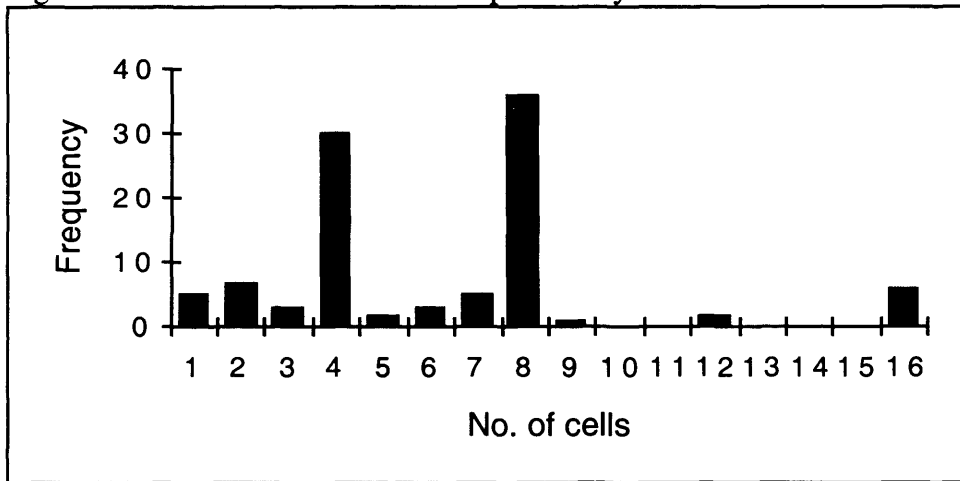
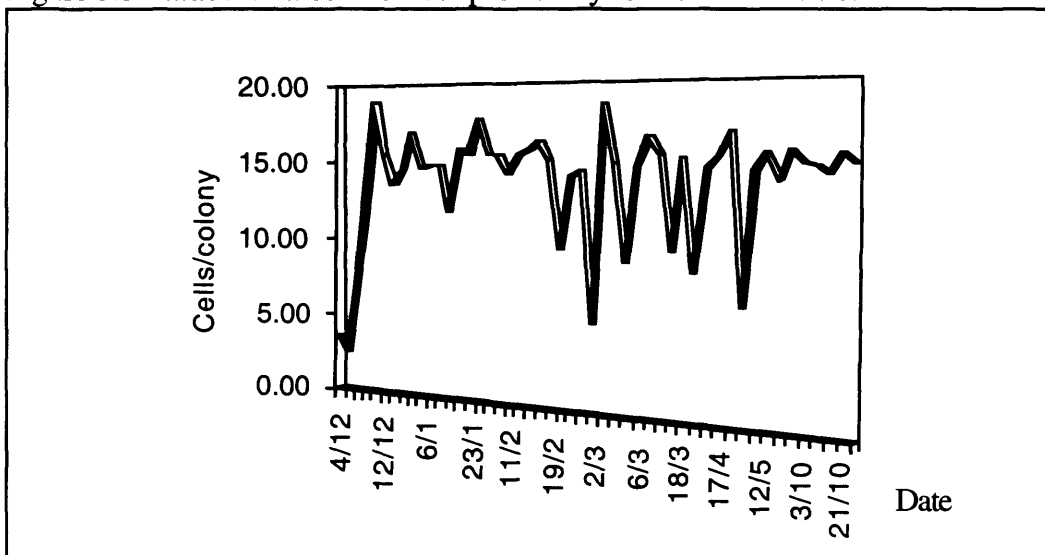


Figure 3.2 *Scenedesmus* cell number per colony.



Mean numbers of cells per colony were also calculated for *Aulacoseira*, however the values obtained varied greatly over time and space. The minimum value was 2.58 cells/colony at site HP surface on 7/12/97 with a maximum of 27.71 cells/colony at site CI 7m depth on 6/1/98. To avoid unnecessary errors whilst investigating community fluctuations and dominance, mean values were not used, especially as *Aulacoseira* is numerically and productively the most important algal genus in Lake Naivasha. Such temporal and spatial fluctuations do not appear to affect mean values as the mean number of cells per colony is 13.97 for the main lake surface, and 13.96 for all sites at all depths sampled. The variation for the main lake surface is shown in Figure 3.3. This indicates that during high *Aulacoseira* periods, cell numbers per colony are greater and more stable than during low *Aulacoseira* periods.

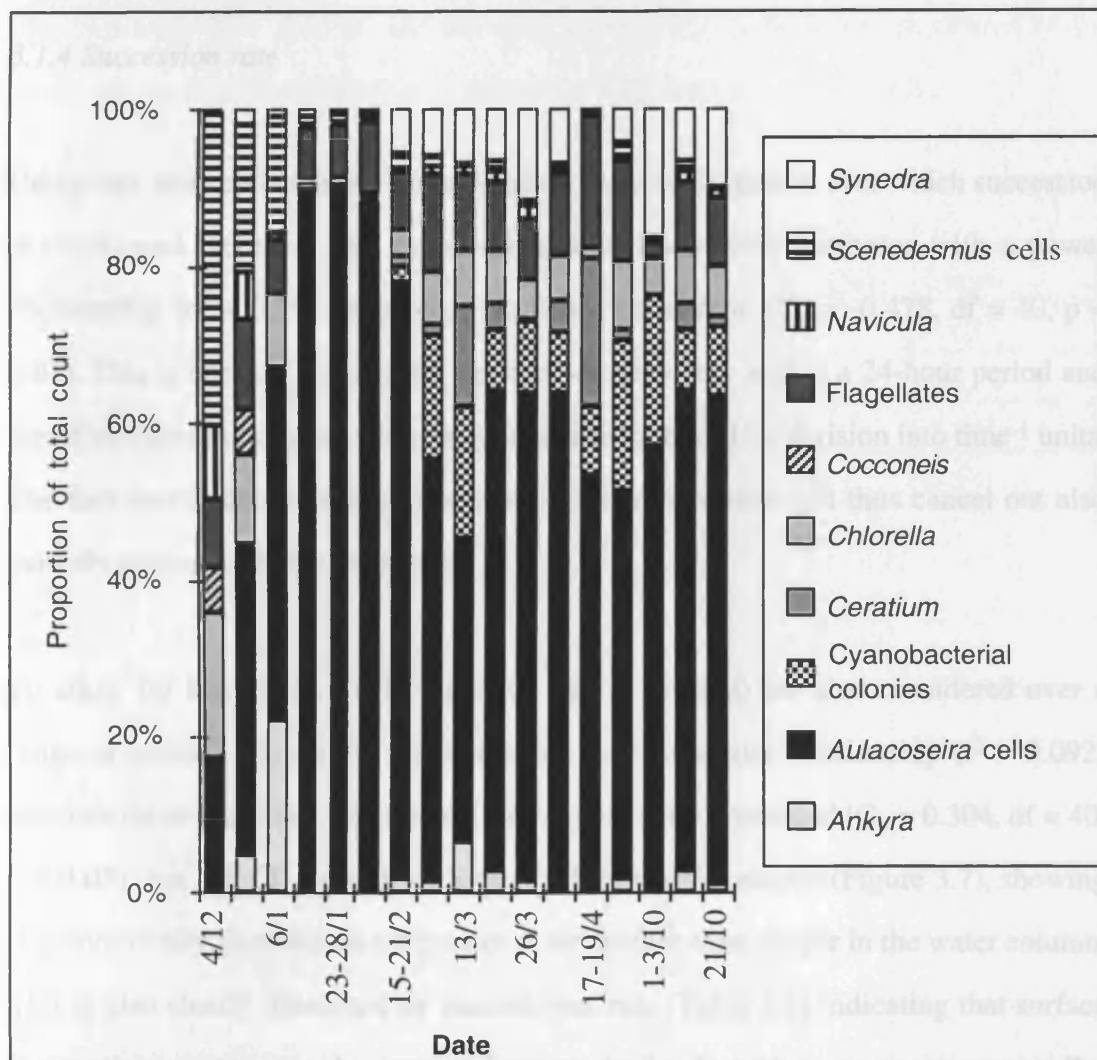
Figure 3.3 *Aulacoseira* cell number per colony 4/12/97 - 21/10/98.



3.1.3 Succession and community fluctuation

When considering dominance and succession, taxa are included which form 10% or more of the assemblage at least once during sampling. This provides the following 'top 10' taxa; *Ankyra*, *Aulacoseira*, cyanobacteria, *Ceratium*, *Chlorella*, *Cocconeis*, flagellates, *Navicula*, *Scenedesmus* and *Synedra*. To simplify the representation of such information, data from consecutive or alternate days are also averaged in Figure 3.4 with only the ten most dominant taxa presented. Of colonial taxa, cyanobacteria are presented as numbers of colonies whilst *Scenedesmus* and *Aulacoseira* are shown as numbers of cells.

Figure 3.4 Main lake algal succession 4/12/97 - 21/10/98.



This shows *Aulacoseira* dominance in main lake surface water for most of the main sampling period (4/12/97 - 21/10/98), although early in this period *Scenedesmus* is more important whilst other members of these 'top 10' taxa contribute variably to the algal assemblage. There is a complex interplay of factors controlling succession, and hence it is not considered relevant to attempt a full explanation of such interactions, although a number of these factors have been identified separately in this chapter. Such factors are determined from both the results obtained and review of standard concepts in the literature. In fact, such an explanation may not be possible, especially considering the variation due to species-specific requirements. An attempt using techniques such as PCA analysis may however provide an interesting area for future work in a more taxonomically-based study.

3.1.4 Succession rate

Using data from cell counts, Figure 3.5 shows that as the period over which succession is considered increases, the calculated rate of succession decreases with a power relationship ($r^2 = 0.596$) showing significant correlation ($C_p = -0.478$, $df = 40$, $p < 0.01$). This is because community fluctuations can occur within a 24-hour period and therefore calculations over a longer timescale are reduced by division into time^{-1} units. The fact that fluctuations may occur in opposite directions and thus cancel out also partially accounts for this relationship.

To allow for this effect, total succession values (S-total) are also considered over a range of periods. Figure 3.6 illustrates that there is a poor relationship ($r^2 = 0.092$) between these quantities, and nor are they significantly correlated ($C_p = 0.304$, $df = 40$, $p > 0.05$). For site CI, a profile of S-total values was developed (Figure 3.7), showing that community fluctuations are greater at the surface than deeper in the water column. This is also clearly illustrated by successional rate (Table 3.1) indicating that surface fluctuations are not only greater in magnitude, but also occur more rapidly.

Hypolimnetic succession rates are also notably lower and less variable than those of surface waters due to two main factors;

1. There is greater physical stability found below the surface as the largely wind-driven mixing processes have a smaller effect deeper in the water column. As many other chemical and physical factors are at least partially regulated by the mixing regime, either through the associated light regime or mixing of waters providing different environmental conditions, there is also greater environmental stability away from the surface layer. This successional profile is therefore not seen in other fully-mixed sampling sites.

2. There is reduced productivity below the optimal photosynthetic depth of approximately 0.5 - 0.75 m, and therefore community fluctuations are slowed by the reduced rates of cellular division, and overall lower numbers of algal cells.

Table 3.1 Succession rate profiles for site CI.

Depth (m)	12/12 - 6/1	6/1-16/1	17/4 - 12/5	3/10 - 13/10	Mean
0	0.055	0.062	0.035	0.076	0.057
1		0.066	0.022	0.018	0.035
3	0.052	0.067		0.011	0.043
7	0.027	0.040	0.027	0.029	0.031

Figure 3.5 Regression of succession rate & period.

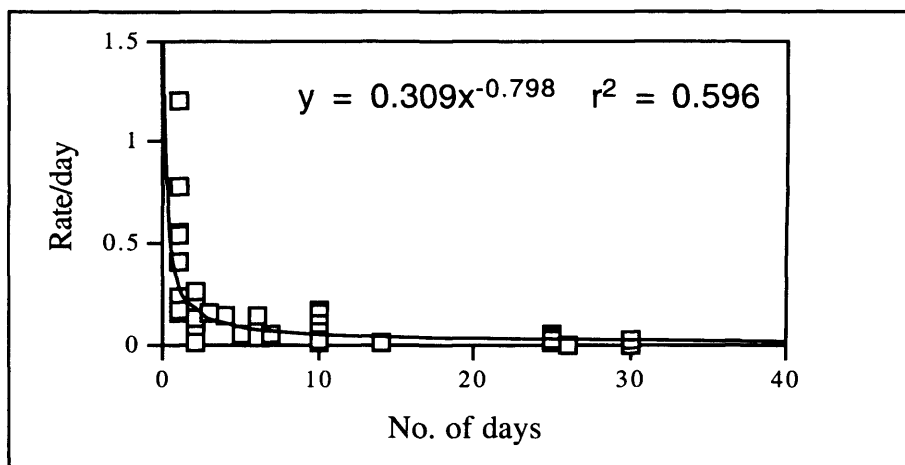


Figure 3.6 Regression of succession total & period.

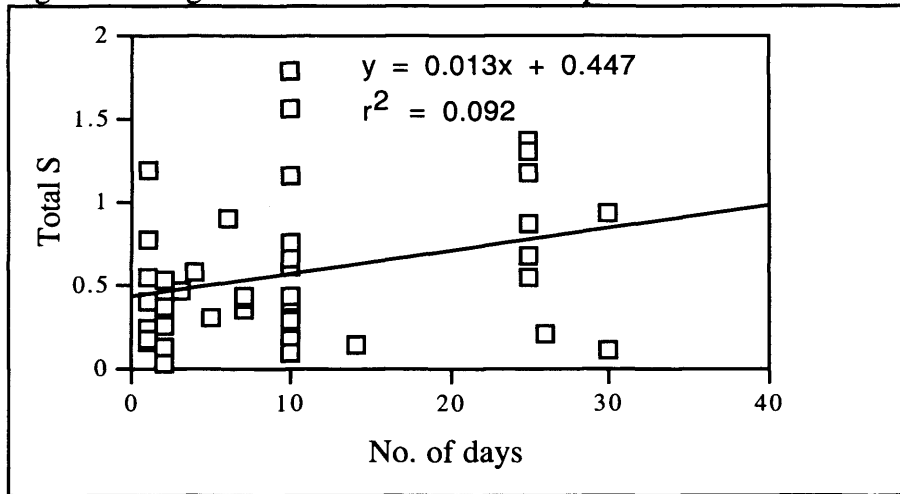
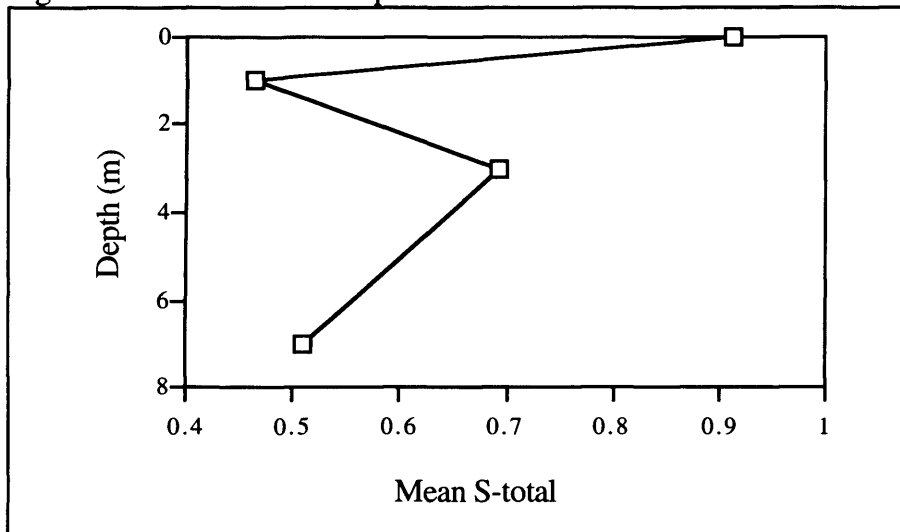


Figure 3.7 Total succession profile for site CI.

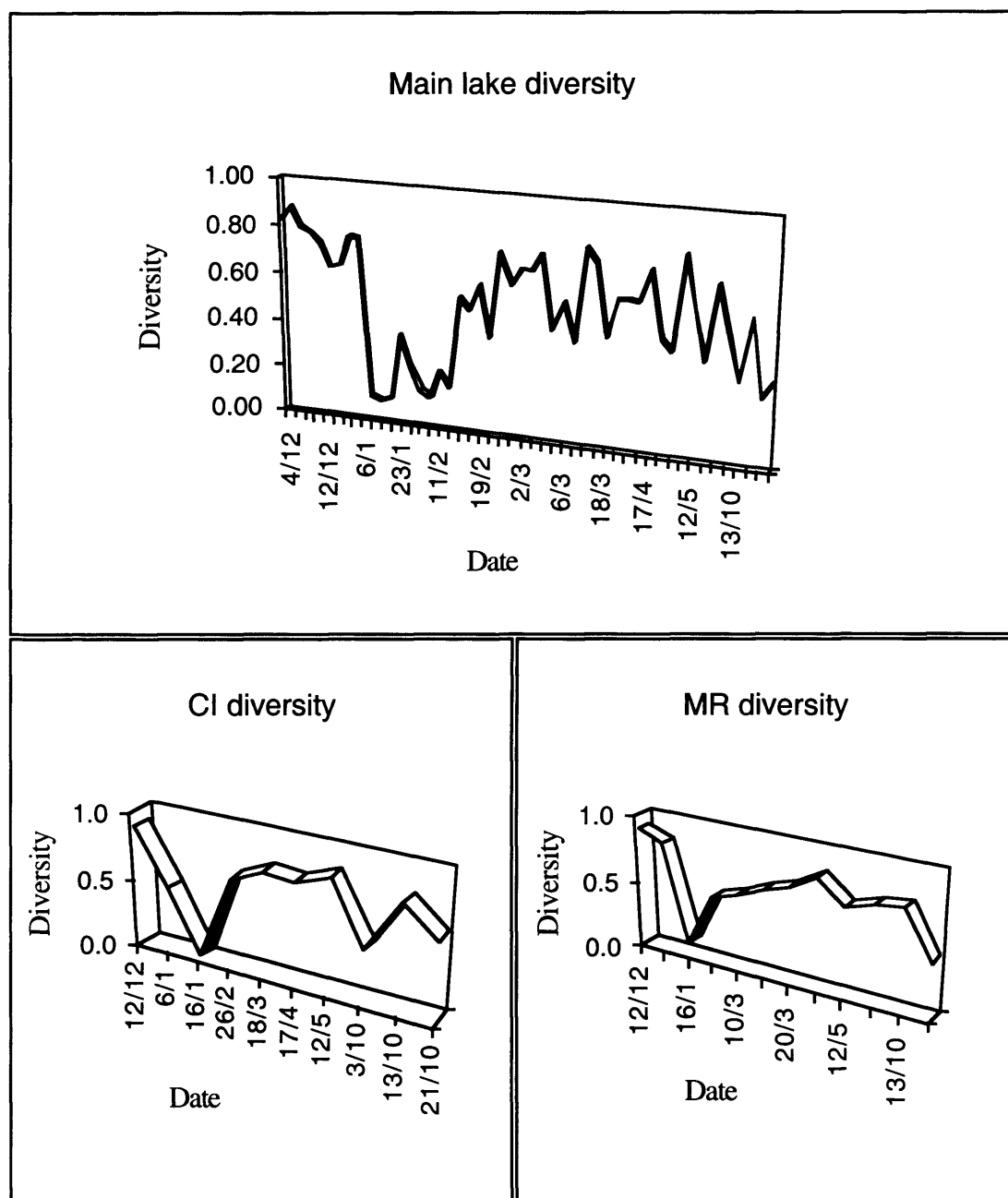


Such rates of succession (as well as indices of ecosystem stability) change as succession progresses as the resulting increased order leads to system predictability and pre-adaptation. There are changes in phytoplankton community structure, however no stages are seen which correlate with nutrient levels. Lake Naivasha is moderately eutrophic and shows diatom dominance with dinoflagellate and cyanobacterial sub-dominance. It therefore fits with the mesotrophic stage expected in temperate waters as many phytoplanktonic species are the found across a range of latitudes. Considerable fluctuations in nutrient levels were measured, but as the pattern of temperate oligotrophic-eutrophic succession is not seen, they are not large enough to constitute a change in trophic state.

3.1.5 Diversity

Simpson's diversity was calculated for all samples, with separation into values for different sites and depths to allow consideration of changes over time and between sites, as illustrated in Figure 3.8. Table 3.2 shows mean values for a number of sites and depths. Site CI is investigated in profile due to its temporarily stratified nature, whilst MR and Main sites are fully mixed, showing no significant vertical variation.

Figure 3.8 Simpson's Diversity 4/12/97 - 21/10/98.



These graphs show a similar pattern of temporal diversity change, with troughs in January 1998 when there was almost total domination by an abundant population of *Aulacoseira*. Diversity was however similar between sites with an overall mean of 0.60, and maxima generally occurring when *Aulacoseira* densities were relatively low, further highlighting the importance of this genus.

Table 3.2 Mean planktonic diversity values.

Site	Mean Diversity	Site	Mean Diversity
Main, surface	0.55	CI, 1m	0.48
MR, surface	0.64	CI, 3m	0.44
CI, surface	0.62	CI, 7m	0.42

To test whether diversity decreases with depth, Table 3.3 shows probability values for one-tailed t-tests, and r^2 regression values comparing diversity at different depths for site CI.

Table 3.3 Site CI diversity comparison between sampling depths.

Cp (prob)	r^2 (1-tailed probability)			
	CI 0m	CI 1m	CI 3m	CI 7m
CI 0m		0.736 (0.029)	0.576 (0.035)	0.564 (0.021)
CI 1m	0.858 (0.01)		0.946 (0.045)	0.876 (0.078)
CI 3m	0.759 (0.05)	0.972 (<0.001)		0.888 (0.387)
CI 7m	0.751 (0.05)	0.936 (<0.001)	0.942 (0.01)	

df = 5 for comparisons with CI 3m, df = 6 for other comparisons.

Table 3.4 Inter-site diversity comparison.

df = 8	r^2 (2-tailed probability)		
Cp (prob)	Main	CI	MR
Main		0.346 (0.323)	0.608 (0.084)
CI	0.588 (0.10)		0.514 (0.738)
MR	<i>0.780 (0.01)</i>	<i>0.717 (0.02)</i>	

Table 3.4 shows the same information (with 2-tailed tests) for comparisons between sites. Italic type indicates significant differences between diversity values, and for all

depth and site combinations, ANOVA gives F-values above the critical limit. There are no significant differences in diversity between sites, suggesting that the processes affecting diversity act equally throughout the lake. Sites CI and Main lake are not significantly correlated and therefore vary separately. Regression is closest between sites MR and Main lake (i.e. when site CI is not being considered); this may be due to the different hydrological regime found at site CI. Depth profiles of site CI are therefore considered separately as illustrated in Figure 3.9, whilst Table 3.5 shows that all CI depths correlate with the Main lake giving $p < 0.001$ for all combinations.

Figure 3.9 Site CI profile of plankton community composition.

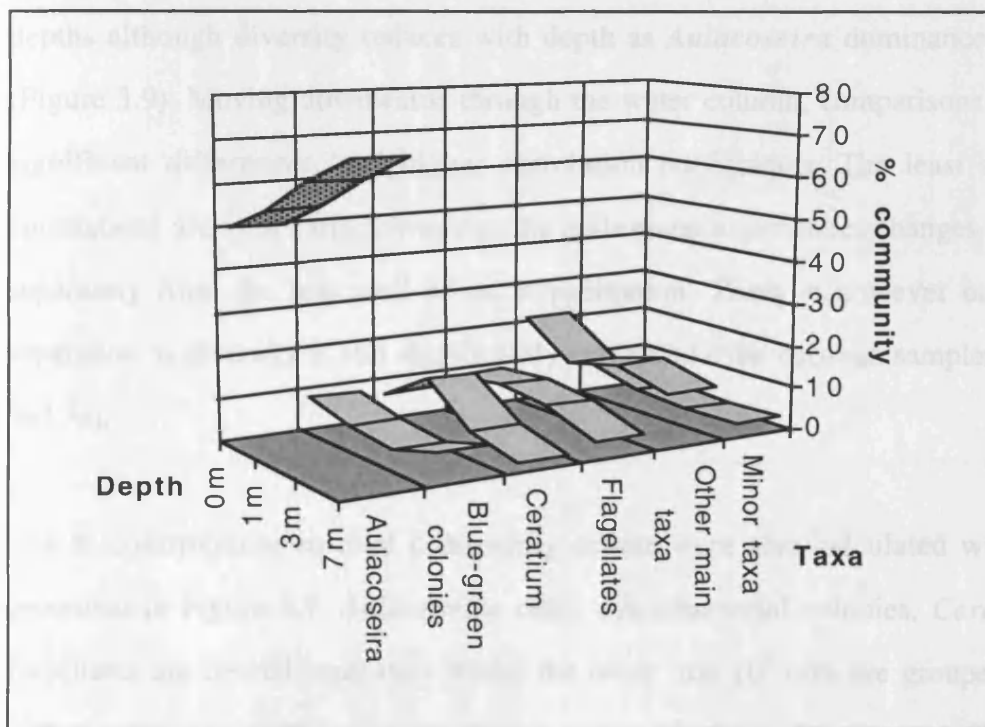


Table 3.5 Inter-site correlation for main species percentage of community.

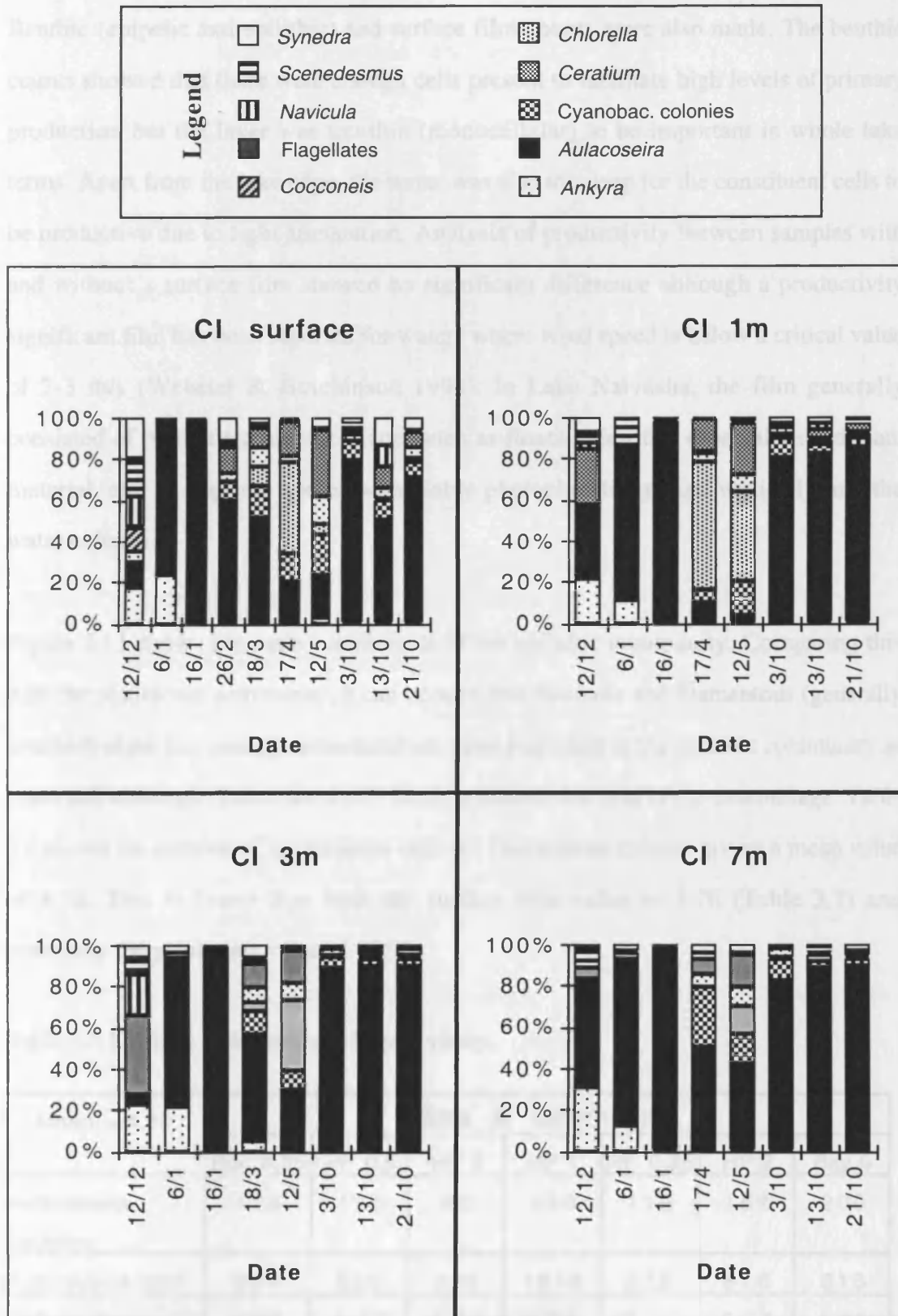
df = 8	CI 0m	CI 1m	CI 3m	CI 7m
CI 0m				
CI 1m	0.985			
CI 3m	0.995	0.985		
CI 7m	0.993	0.973	0.994	
Main 0m	0.995	0.973	0.993	0.994

Comparing Figures 3.8 and 3.10 shows that low diversity periods equate to high *Aulacoseira* periods as this genus may comprise over 90% of the algal community. Such periods are seen during January and October 1998, whilst high diversity - low *Aulacoseira* periods are seen during December 1997 and April - May 1998. However, the causes of such large changes in *Aulacoseira* abundance are as yet unknown.

Considering spatial variations in diversity, vertical differences at site CI are detailed in Tables 3.2 and 3.3. These show that hypolimnetic diversity is lower than that in the epilimnion due to the more physically stressed conditions caused primarily by light attenuation. The most significant differences are between 0m and the other sampled depths although diversity reduces with depth as *Aulacoseira* dominance increases (Figure 3.9). Moving downwards through the water column, comparisons show less significant differences, and higher correlation coefficients. The least significant correlations are with surface water as the epilimnion experiences changes somewhat separately from the less well-mixed hypolimnion. There is however only partial separation as diversity is still significantly correlated even between samples from 0m and 7m.

The % contributions to total community counts were also calculated with results presented in Figure 3.9. *Aulacoseira* cells, cyanobacterial colonies, *Ceratium* and flagellates are treated separately whilst the other 'top 10' taxa are grouped to form 'Other main taxa' with remaining genera grouped to form 'Minor taxa'. This shows *Aulacoseira* forming approximately 50% of the surface community and 70% at a depth of 7m. The 'Other main taxa' (i.e. those which are sometimes dominant or sub-dominant) form 10 - 20% of the community, with the remaining groups in small, fairly equal proportions. Correlating % community counts (Table 3.5) shows that although absolute abundance of taxa may vary, proportional community structure is closely linked both vertically and between sites as $p < 0.001$ for all combinations.

Figure 3.10 Site CI community succession with depth (Dec 1997 - Oct 1998).



3.1.6 Benthic and surface films

Benthic (epipellic and epilithic) and surface film counts were also made. The benthic counts showed that there were enough cells present to facilitate high levels of primary production but the layer was too thin (monocellular) to be important in whole lake terms. Apart from the lake edge, the water was also too deep for the constituent cells to be productive due to light attenuation. Analysis of productivity between samples with and without a surface film showed no significant difference although a productivity significant film has been reported for waters where wind speed is below a critical value of 2-3 m/s (Webster & Hutchinson 1994). In Lake Naivasha, the film generally consisted of particulate organic matter such as floating detritus, especially dead plant material, and *C. papyrus* spores with viable phytoplankton mixed vertically into the water column.

Figure 3.11 shows the main constituents of the epilithic community. Comparing this with the planktonic community, it can be seen that *Navicula* and filamentous (generally attached) algae (i.e. non-cyanobacteria) are more important in the epilithic community as expected, although *Aulacoseira* still forms a notable fraction of the assemblage. Table 3.6 shows the number of *Aulacoseira* cells per filamentous colony, giving a mean value of 4.70. This is lower than both the surface film value of 5.76 (Table 3.7) and especially the planktonic value of 13.96.

Table 3.6 Epilithic *Aulacoseira* cells per colony.

Mean = 4.70	Site & depth (m)						
	Bay 0.25	HP 0.5	HP 3	HP 1	HP 0.25	HP 2	Bay 0
<i>Aulacoseira</i> colonies	128	120	80	360	112	152	200
<i>Aulacoseira</i> cells	624	560	336	1648	576	816	816
Cells/colony	4.88	4.67	4.20	4.58	5.14	5.37	4.08

Figure 3.11 Main lake epilithic algal community October 1998.

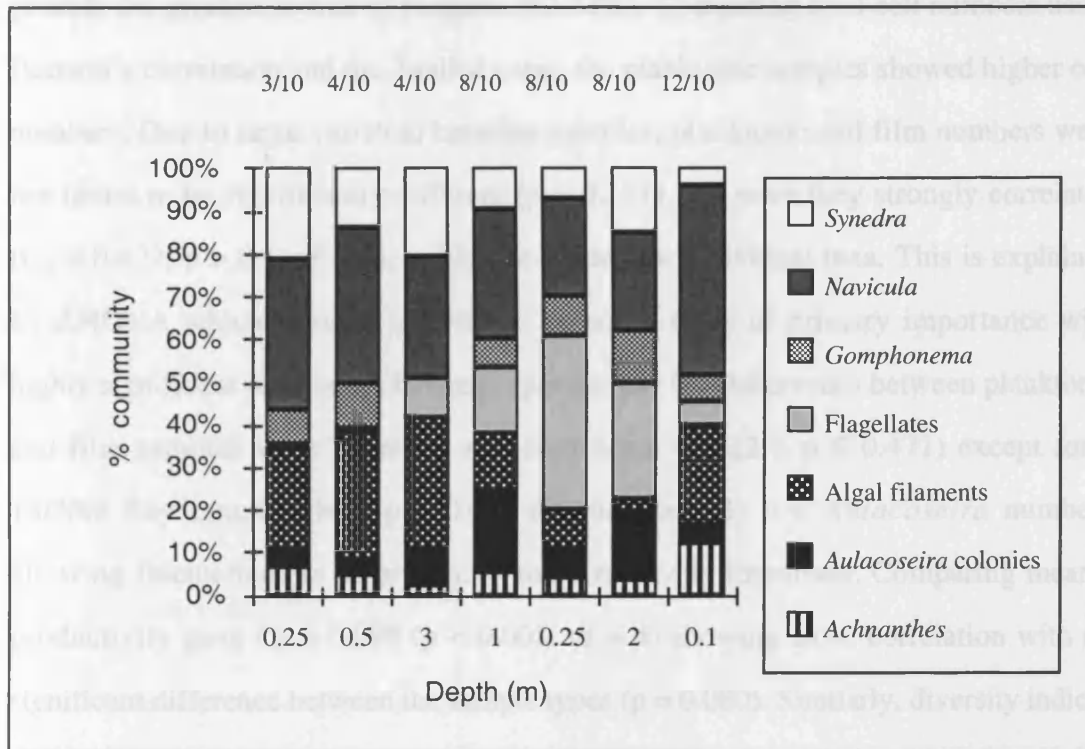


Table 3.7 Surface film *Aulacoseira* cells per colony.

Mean = 5.76	Site					
	Bay	Bay	MR	MR	MR	Bay
<i>Aulacoseira</i> colonies	752	288	72	360	112	72
<i>Aulacoseira</i> cells	5760	1632	448	1872	624	304
Cells/colony	7.66	5.67	6.22	5.20	5.57	4.22

Planktonic surface water samples with and without the surface film were compared to investigate whether the film had a significant effect on community composition or productivity, the data being presented in Table 3.8 where community counts for all individual taxa are compared using Spearman rank correlation (C_s). This shows planktonic and film counts to be highly correlated with values ranging from $C_s = 0.817$ to $C_s = 0.999$. All samples showed a significant difference between cell concentration with the surface film having lower taxon cell numbers ($p < 0.01$, $df = 44$ for all samples). *Aulacoseira* was however still dominant and was the source of most variance

(69.90% to 95.53%) in all samples except site MR on 13/10/98 where flagellates provide the greatest source of variance (62.33%). Comparing total cell numbers using Pearson's correlation and the 2-tailed t-test, the planktonic samples showed higher cell numbers. Due to large variation between samples, planktonic and film numbers were not found to be significantly different ($p = 0.151$), nor were they strongly correlated ($C_p = 0.427$, $p > 0.1$, $df = 4$), unlike the values for individual taxa. This is explained by ANOVA which showed inter-taxon variation to be of primary importance with highly significant differences between species ($p \approx 0$). Differences between planktonic and film samples were generally non-significant ($0.122 \leq p \leq 0.471$) except for a 18/3/98 Bay sample where $p = 0.003$ due to relatively low *Aulacoseira* numbers allowing fluctuations in other species to be relatively important. Comparing means, productivity gave $C_p = 0.998$ ($p < 0.001$, $df = 4$) showing close correlation with no significant difference between the sample types ($p = 0.080$). Similarly, diversity indices between the sample types showed close correlation ($C_p = 0.909$, $p < 0.02$, $df = 4$) and no significant difference ($p = 0.600$).

Table 3.8 Comparison of productivity, diversity and cell numbers between planktonic and surface film samples.

Site/Date	C_s	Productivity		Diversity		Cell totals	
		Plankton	Film	Plankton	Film	Plankton	Film
MR 6/3	0.985	116.26	115.16	0.51	0.54	11628	2884
MR 18/3	0.819	203.12	197.38	0.65	0.61	8984	2904
Main 18/3	0.930	113.61	115.78	0.87	0.78	1388	748
Main 12/5	0.984	115.24	110.20	0.41	0.60	3356	2644
Main 12/10	0.999	123.84	121.34	0.27	0.28	7104	6788
MR 13/10	0.817	113.42	110.19	0.76	0.79	1568	2220
Mean		130.92	128.34	0.58	0.60	5671	3031

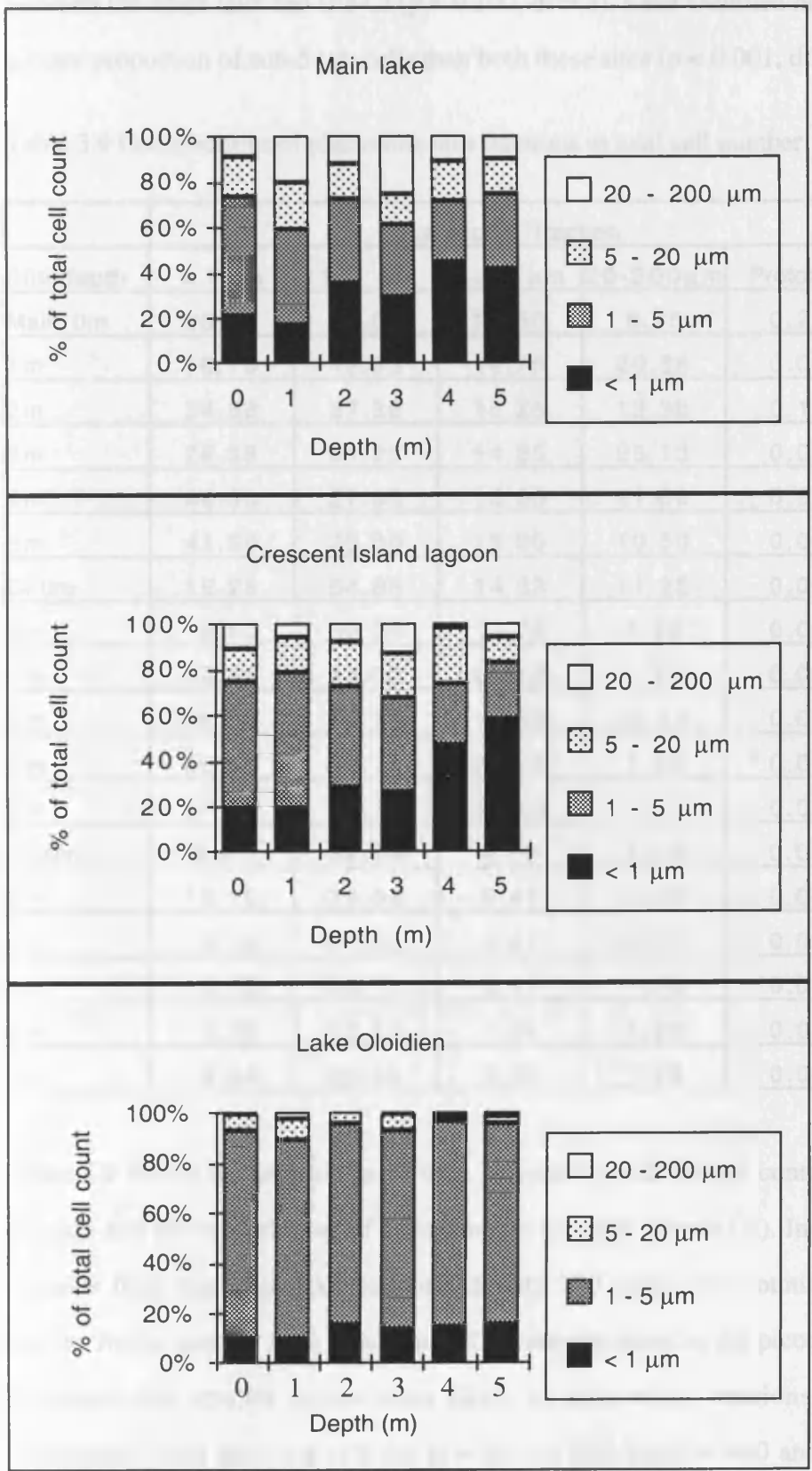
Comparing planktonic and film productivity for the 6 samples (5 replicates in each), t-tests show no significant difference between these sample types, however neither are they strongly correlated ($C_p = 0.023$ to 0.548 , $p > 0.1$, $df = 3$) except for the 6/3/98 sample at site MR where $C_p = 0.929$ ($p < 0.05$, $df = 3$).

Sediment cores gave benthic counts (cm^{-2}) and sediment-water counts (ml^{-1}) as presented in Appendix 5. Benthic and sediment-water results were highly correlated for both sites Bay and OW ($C_p = 0.983$ & $C_p = 0.984$ respectively) as were the sites themselves ($C_p = 0.993$ for benthic counts & $C_p = 0.984$ for sediment-water counts). For all these correlations, $p < 0.001$ ($df = 46$) indicating a high level of significance. ANOVA also indicates that whilst sediment-water counts showed no significant differences between sites ($p = 0.241$), benthic counts were different ($p = 0.037$) with the Bay count being lower. *Aulacoseira* provides the largest amount of variance in sediment-water counts (94.48%), whilst for sediment samples this is due to *Navicula* (44.10%).

3.1.7 The microbial loop

Conventionally, pico- and nanno-plankton are those with cells of size $0.2 - 2 \mu\text{m}$ and $2 - 20 \mu\text{m}$ respectively. During preliminary counts however, many cells including important taxa such as *Microcystis* were measured at $1 - 3 \mu\text{m}$ and were difficult to place in either group with certainty. Determined visually, nannoplankton were therefore taken to be $5 - 20 \mu\text{m}$, picoplankton $1 - 5 \mu\text{m}$, and the fraction with cells smaller than $1 \mu\text{m}$ formed the 'attoplankton'. Figure 3.12 illustrates the proportions of the plankton community attributed to each size fraction for the three sites sampled. Protozoa are not included as too few were present to allow illustration. Both the Main lake and site CI show an increase in attoplankton coupled with a decrease in picoplankton ($C_p = -0.793$, $p < 0.05$, $df = 5$ and $C_p = -0.941$, $p < 0.01$, $df = 5$ respectively). No such relationship is seen in Lake Oloidien ($C_p = -0.136$, $p > 0.1$, $df = 5$) with the picoplankton dominant at all depths and the proportions of all other fractions consequently reduced. The nanno- and micro-plankton do not show trends with depth for any of the sites. The atto- and pico-plankton combined form a stable fraction of the community with the mean percentage and standard deviation of cells below $5 \mu\text{m}$ being 68.63% ($s = 6.77$), 74.56% ($s = 5.39$) and 93.64% ($s = 2.75$) for the Main lake, site CI and site OL respectively ($n = 6$).

Figure 3.12 Contributions of size fractions to cell numbers in the plankton community.



A 2-tailed t-test shows no significant difference in the proportion of sub-5 μm cells between the Main lake and site CI ($p = 0.100$, $df = 5$). Lake Oloidien however shows a greater proportion of sub-5 μm cells than both these sites ($p < 0.001$, $df = 5$).

Table 3.9 Contributions of planktonic size fractions to total cell number.

Site/depth	Planktonic fraction					N
	< 1 μm	1-5 μm	5-20 μm	20-200 μm	Protozoa	
Main 0m	20.88	52.63	17.50	8.75	0.25	400
1m	16.75	42.63	19.75	20.88	0.00	400
2m	34.88	37.38	15.25	12.38	0.13	400
3m	29.38	31.25	14.25	25.13	0.00	400
4m	44.50	27.00	16.50	11.50	0.50	200
5m	41.50	33.00	15.00	10.50	0.00	200
CI 0m	19.25	54.88	14.63	11.25	0.00	400
1m	18.50	60.00	15.75	5.75	0.00	400
2m	28.13	44.00	20.13	7.75	0.00	400
3m	26.38	40.50	19.63	13.50	0.00	400
4m	46.50	26.75	25.25	1.50	0.00	200
5m	57.75	24.75	11.50	6.00	0.00	200
OL 0m	9.81	82.81	6.09	1.28	0.00	1600
1m	10.16	79.06	8.41	2.38	0.00	1600
2m	15.19	80.00	4.41	0.31	0.09	1600
3m	13.72	78.75	6.41	1.09	0.03	1600
4m	14.59	82.19	1.84	1.34	0.03	1600
5m	14.94	80.63	2.69	1.75	0.00	1600

Table 3.9 shows the percentage of total community cell counts contributed by each fraction and the total number of cells counted for each sample (N). In the 4m and 5m samples from the Main lake and site CI only 200 cells were counted as few were visible. In the samples from Oloidien, 1600 were estimated as the picoplankton was so dominant that smaller counts were likely to miss other fractions entirely. 95% confidence limits are $\pm 14.14\%$ for $N = 200$, $\pm 10\%$ for $N = 400$ and $\pm 5\%$ for $N = 1600$. All samples contained few, if any, protozoa.

Table 3.10 gives the comparison between sites for the proportion of each planktonic fraction. For each fraction, P_t is the probability value from a 2-tailed t-test comparing sites, and P_c is the probability value from Pearson correlation of sites.

Table 3.10 Inter-site comparison and correlation of proportions of planktonic fractions.

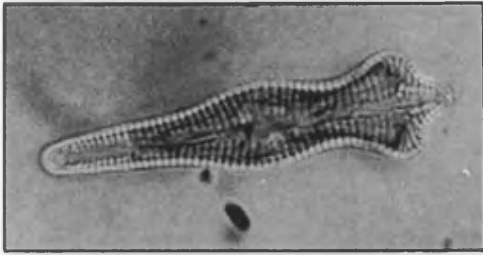
Sites	Planktonic fraction			
	< 1 μm (atto)	1 - 5 μm (pico)	5 - 20 μm (nanno)	20 - 200 μm (micro)
CI vs Main	$P_t = 0.676$ $P_c < 0.01$	$P_t = 0.263$ $P_c < 0.05$	$P_t = 0.553$ $P_c > 0.1$	$P_t = 0.037$ $P_c > 0.1$
OL vs Main	$P_t = 0.004$ $P_c < 0.01$	$P_t \approx 0$ $P_c > 0.1$	$P_t \approx 0$ $P_c > 0.1$	$P_t = 0.004$ $P_c > 0.1$
CI vs OL	$P_t = 0.020$ $P_c > 0.05$	$P_t = 0.001$ $P_c > 0.1$	$P_t = 0.004$ $P_c > 0.1$	$P_t = 0.019$ $P_c > 0.1$

Lake Oloidien shows a significantly greater proportion of picoplankton than the Main lake and site CI, but a significantly lower proportion of all other fractions. There is no significant difference in the proportions of any fractions between the Main lake and site CI. The proportion of attoplankton in the Main lake is significantly correlated with that of the other sites as all show an increase in attoplankton with depth. A significant correlation of picoplankton proportion between site CI and the Main lake is also seen as both show a decrease in picoplankton with depth.

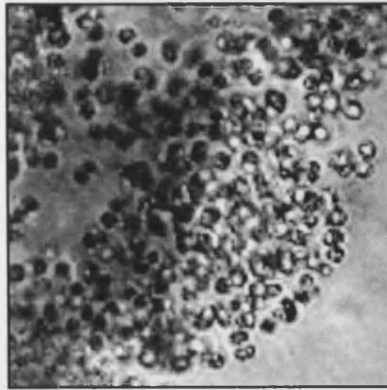
Plates

Plate I. Some phytoplankton of Lake Naivasha

Gomphonema acuminatum

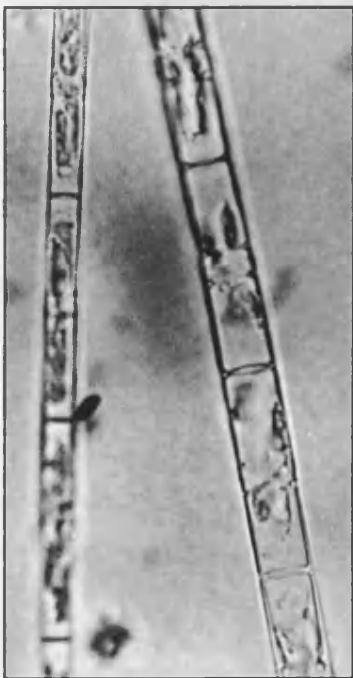


|——| 10 μm (x 400)



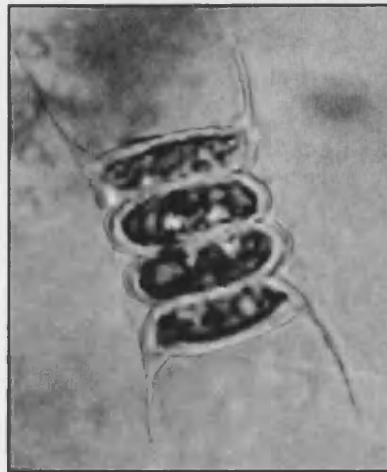
|——| 10 μm (x 400)

Aulacoseira italica & *A. granulata*



|——| 10 μm (x 400)

Scenedesmus protuberans



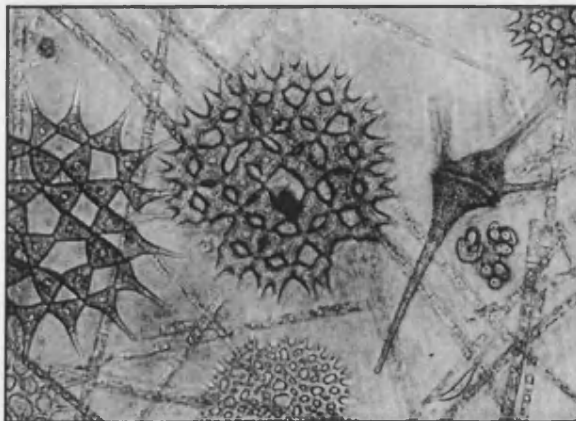
|——| 10 μm (x 400)

A mixture of phytoplankton including *Ceratium*, *Pediastrum*, *Ankyra* and abundant *Aulacoseira*.

Anabaena sp.



|——| 10 μm (x 400)

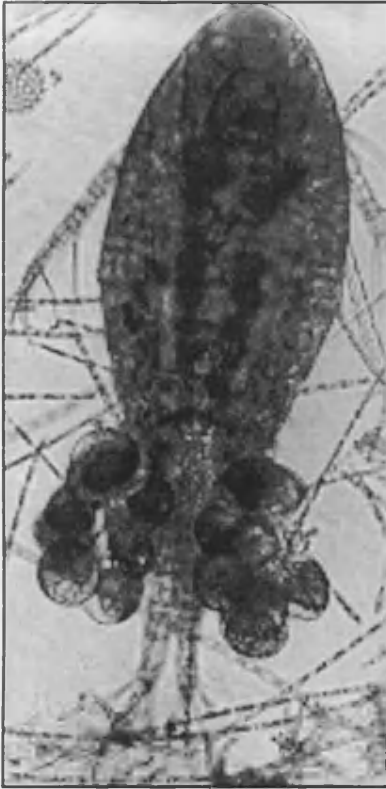


|——| 30 μm (x 200)

Microcystis sp.

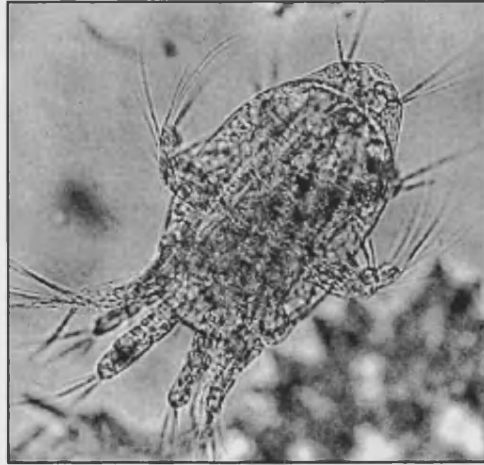
Plate II. Some zooplankton of Lake Naivasha

Female *Cyclops* with egg sacs



|——| 0.1mm (x 100)

Nauplius larva of *Cyclops*



|——| 0.1 mm (x 200)

Females of the polymorphic rotifer, *Brachionus calyciflorus* (x 200)

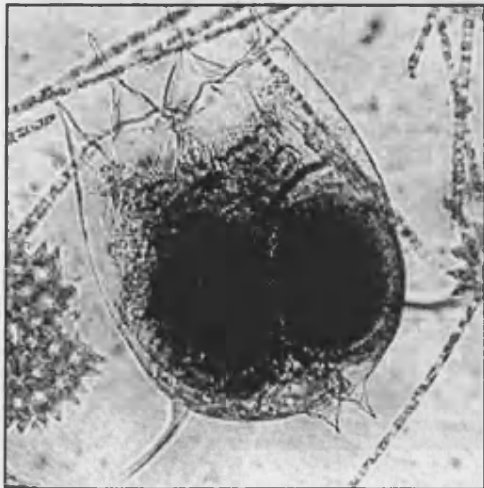


|——| (a) 50 μ m, (b) 80 μ m

Daphnia sp.



|——| 0.1mm (x 100)





1. Inflow of River Malewa through *Cyperus papyrus* swamp to site MR.



2. Dam on River Turasha, the main tributary of River Malewa.



3. River Malewa showing small-scale agriculture and erosion on steep banks.



4. River Malewa 4km from its inflow into Lake Naivasha.



5. Lake Oloidien with the edge of Lake Naivasha in the foreground.



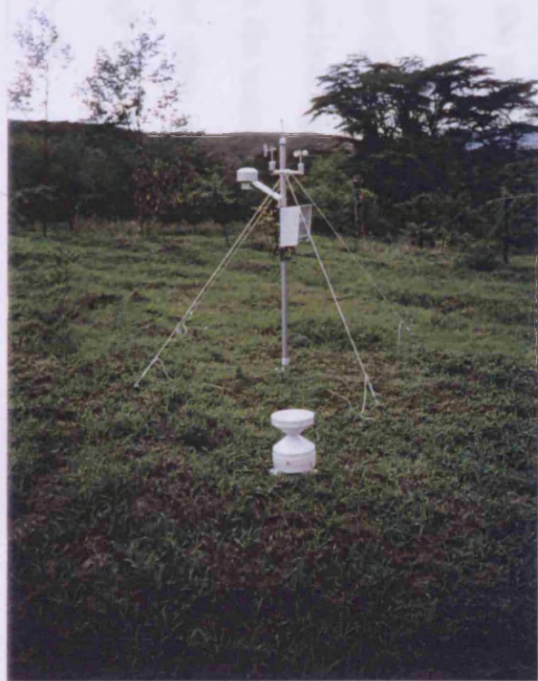
6. Crescent Island lagoon during low lake level.



7. Floating *Eichhornia crassipes* on Lake Naivasha.



8. Fringing vegetation around Lake Naivasha.



9. Site of the automatic weather station.



10. Intensive floriculture near the edge of Lake Naivasha.



11. Irrigated field in the Naivasha catchment.

4. Chemical and Physical conditions

When considering the management of a lake and its ecosystem, we like to know the processes describing the sources, transport mechanisms and reservoirs for every substance entering the lake. The main transport routes are the atmosphere, rivers and anthropogenic inputs.

For instance the particulate load of rivers is approximately 3 - 5 times the dissolved load (Stumm & Baccini 1978) with materials originating from erosion, chemical denudation and human activities including land-use changes. Such changes are largely understandable if the environmental history of the water, its pollution, and the rock-water-atmosphere systems are considered. Essentially, the latter forms the focus of this study along with the interactions between organisms and both their biotic (grazing pressure, competition & self-shading) and abiotic (chemistry, hydrology & climate) environments as measured in terms of primary productivity.

As well as algal nutrients, other substances such as organic compounds, acidifying materials and heavy metals may have impacts not directly relevant to this study although the latter is often correlated with phosphorus loading through sediment transport. Both the suspended and benthic sediments of a lake are important in developing an understanding of the numerous processes occurring within the system as a whole. When considering productivity controls, sediments may therefore be described in terms of storage and recycling of both organic and inorganic substances, although the fate of organic matter is not investigated here. Gaudet & Melack (1981) indicated that sediment exchange provides the major source of input (51 - 86%) and output (84 - 98%) of all minor nutrients and other ions for Lake Naivasha. Other inputs include seepage (7 - 30%), river water (5 - 25%) and rain (up to 1.4%), whilst seepage forms the only other output (2 - 16%).

4.1 Results

4.1.1 Sedimentation loss

After 4 hours, there is relatively little reduction in productivity (12.26%), but after 8 hours, there is a 77.83% decrease in productivity due to sedimentation loss (Table 4.1). Using one-tailed paired t-tests, there was no significant reduction in productivity over the first 4 hours ($p = 0.076$), whilst over the next 4 hours there was highly significant reduction ($p \approx 0$). There was little further change beyond 8 hours of sedimentation. Correlation coefficients ($df = 3$) show no relationship between productivity at 0 and 4 hours ($C_p = -0.109$, $p > 0.1$) but a strong relationship between 4 and 8 hours ($C_p = 0.957$, $p < 0.02$). Variations in productivity therefore may occur between 0 and 4 hours without any significant sedimentation loss. After this point there would be a large decrease in productivity through sedimentation.

Table 4.1 Productivity loss by experimental sedimentation of algal cells.

Sample	0 hours	4 hours	8 hours	0-4 hrs % red'n	0-8 hrs % red'n	4-8 hrs % red'n
1	104.49	101.59	26.04	-2.78	-75.08	-74.37
2	103.08	95.72	24.54	-7.14	-76.19	-74.36
3	120.88	108.92	30.04	-9.89	-75.15	-72.42
4	130.60	92.44	19.74	-29.22	-84.89	-78.65
Mean	114.76	99.67	25.09	-12.26	-77.83	-74.95
St. Dev.	6.65	3.62	2.13	5.84	2.37	1.32

Losses to cell numbers from taxa which form an important fraction of the algal assemblage (table 4.2) show where productivity losses mainly occur (the complete data set can be found in Appendix 6). Taxa showing increased cell numbers are included for comparison. The most important sedimentation effect is that the dominant genus *Aulacoseira* lost 47.76% of cells within the first 4 hours and a 93.15% over 8 hours. Cyanobacteria only lost 15.05% and 57.35% respectively, whilst other important taxa lost between 59.84% (*Synedra*) and 96.88% (*Scenedesmus*) of cells over 8 hours. Motile flagellates and *Staurastrum* showed increased cell numbers.

Table 4.2 Changes in planktonic cell numbers by sedimentation.

Taxon	% change 0 - 4 hours	% change 0 - 8 hours
<i>Ankistrodesmus</i>	-46.77	-42.74
<i>Ankyra</i>	-43.48	-76.09
<i>Aulacoseira</i> colonies	-37.67	-92.56
<i>Aulacoseira</i> cells	-47.76	-93.15
Blue-greens	-15.05	-57.35
<i>Chlorella</i>	-36.36	-90.91
Flagellates	+35.16	+7.03
<i>Mallomonas</i>	+106.90	+72.41
<i>Scenedesmus</i>	-18.75	-96.88
<i>Staurastrum</i>	+45.45	+27.27
<i>Synedra</i>	-26.77	-59.84

A number of genera showed a total loss of cells over an 8-hour period, namely *Amphora*, *Closterium*, *Cosmarium*, *Crucigenia*, *Cymbella*, *Epithemia* and *Fragilaria*, whilst others showed losses ranging from 33.33% (*Gomphonema*) to 81.25% (*Navicula*). These were again all found in small numbers initially, indicating that values of percentage change may be inaccurate. In order to include these 'minor' taxa, values of mean percentage change per taxon were calculated for the first 4 and 8-hour periods. Data for *Amphora* were however omitted due to a 4-hour increase from 4 to 32 cells/ml giving a large outlying value of +700% change which spuriously returns a mean cell increase for the first 4-hour period. Total cell counts and the related percentage change values were also calculated which avoided such problems with outlying data. Mean percentage change gave losses of 25.04% and 63.13% for 4 and 8-hour sedimentation periods respectively, whilst total cell counts gave losses of 38.00% and 81.41% for the same periods. This pattern follows that of productivity reduction through sedimentation although the 4-hour period shows a smaller reduction in productivity (12.26%) than cell numbers (38.00%).

4.1.2 Background chemistry and physical conditions

Using paired-sample t-tests to compare Secchi depth and conductivity measurements between sites CI, MR and Main lake, all combinations showed significant differences

except for conductivity between MR and Main lake ($p = 0.2$). MR samples were often taken 'downstream' from the true rivermouth due to impenetrable blockage by floating *C. papyrus* islands. Genuine rivermouth conductivity was generally lower than that of the lake as illustrated by results from transects (Figure 4.1), although for a few days around 18/3/98 site MR showed higher conductivity & pH than the rest of the lake as well as the highest concentrations of chlorophyll *a* (133.50 $\mu\text{g/l}$) measured during the entire study. This was largely due to wind-induced accumulation of *Ceratium* cells (3008 cells/ml), although *Aulacoseira* and *Peridinium* were also notably more numerous than in other parts of the lake. Monitoring data showed 56 cells/ml and 26.17 $\mu\text{g/l}$ Chl *a* on 10/3/98, with 328 cells/ml and 46.08 $\mu\text{g/l}$ Chl *a* remaining on 20/3/98. This was therefore an isolated short-term effect without whole-lake importance. Dinoflagellates were also found at higher cellular concentrations than in any other samples throughout the study.

The results for October 1998 are taken during the period around 2/10/98 which showed conditions closest to temporary stratification in the Main Lake with DO levels at 5m depth in site HP falling from 6.0 mg/l at the surface to 2.5 mg/l at 5m. There was however no further deoxygenation below this nor any evidence of sediment nutrient release. Flow from the River Malewa also produced an underflow affecting the vertical profile of conditions around site MR. This is shown by monitoring data although the March 1998 results do not follow this general pattern. This effect can not be determined from nutrient measurements as any increase with depth could be due to sediment-water interactions and/or accumulation through reduced algal activity as well as riverine input. Measurements of conductivity and pH however generally showed reduced levels at 3m depth due to the flow of fresher, more neutral river water beneath the surface layer of the lake. Values of conductivity from samples ($n = 5$) taken at the surface and 3m depth were compared. For site MR and a point 100m towards the lake centre, $p < 0.001$ indicated a high degree of difference between surface and deeper water.

Figure 4.1 Conductivity & pH transects across Lake Naivasha.

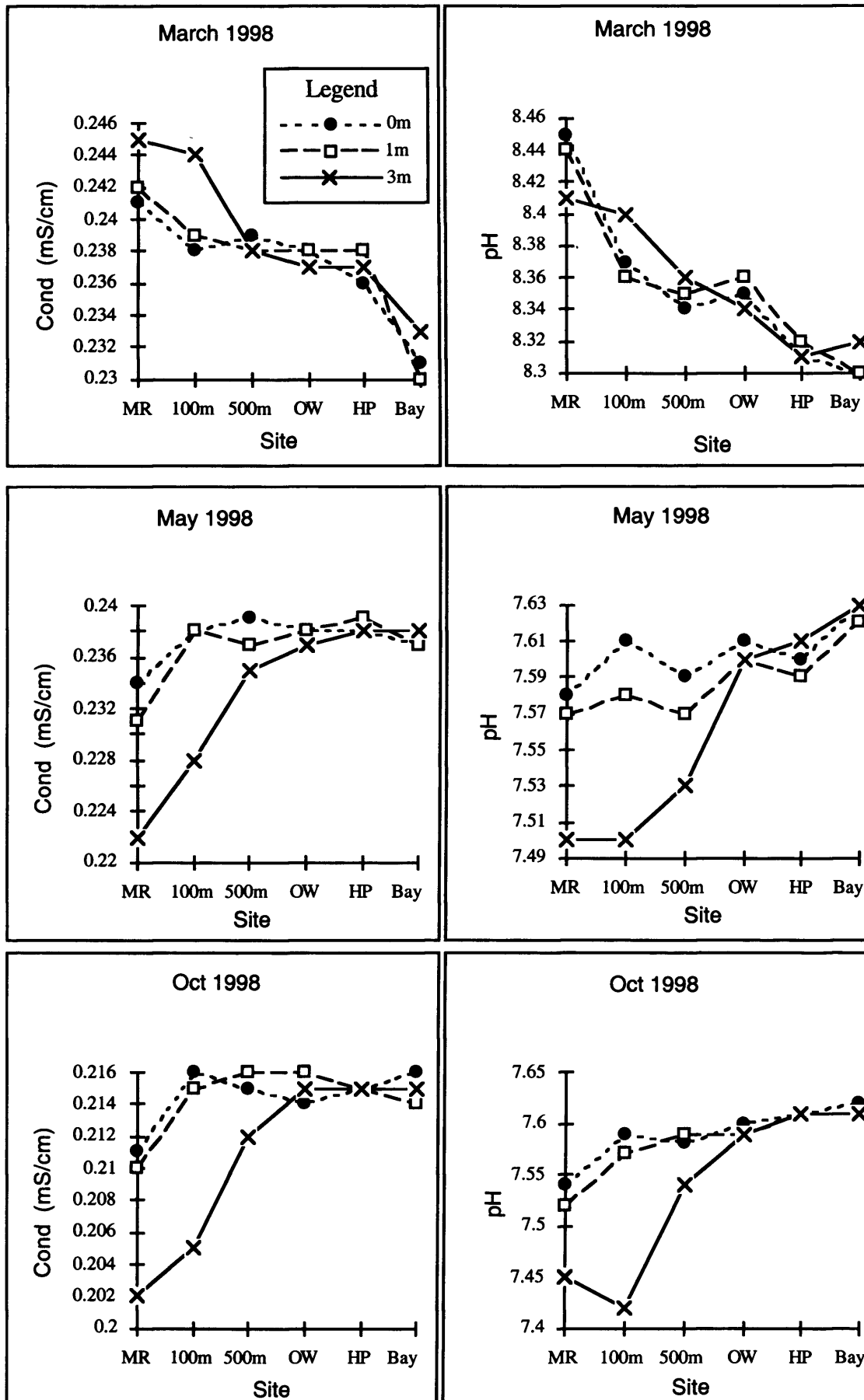
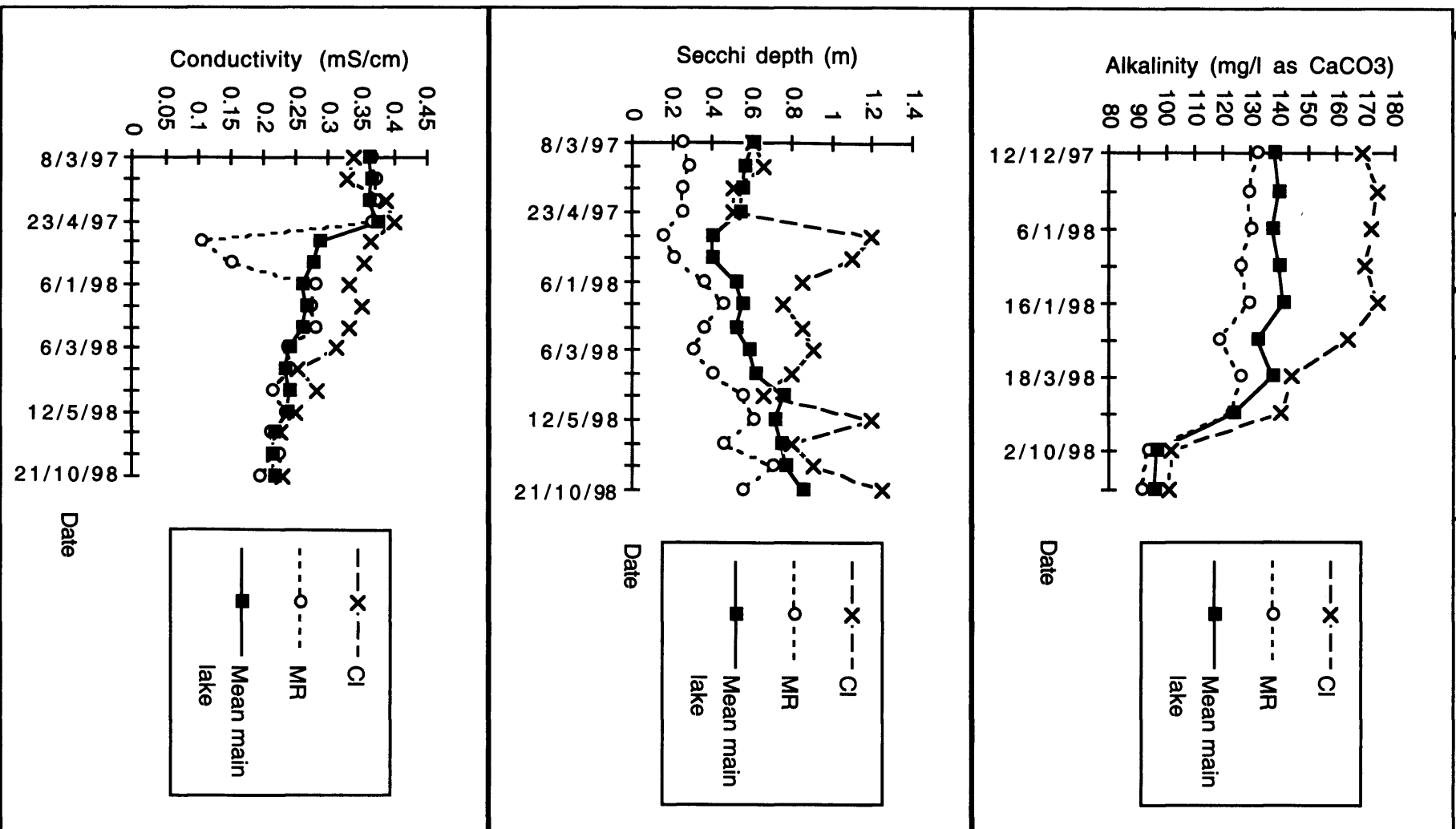


Figure 4.2 Alkalinity, transparency & conductivity time series.



Other parameters however did not follow patterns of deoxygenation or nutrient accumulation and thus underflow must be occurring. This is supported by the fact that differences with depth near the Malewa follow river conditions rather than those of the Main Lake. Gaudet & Melack (1981) produced conductivity data from sampling between 1973 and 1975 when the greatest depth in the Main Lake was site HP at 9m which can be compared with data from this study (Table 4.3).

Table 4.3 Conductivity changes 1973 to 1998.

Site	Conductivity ($\mu\text{S}/\text{cm}$)			
	1973 - 75	April 1997	Jan 1998	Oct 1998
Malewa	120	116	103	
Gilgil	131	171		
CI	457	401	331	226
Oloidien	983	2780	2830	
Main	363	372	260	215

Major changes include the salinisation of Lake Oloidien since its separation from the Main Lake outflow and subsequent development towards soda lake conditions. With increased dilution through a rise in lake level, CI and the Main Lake have become less saline, whilst the Malewa showed a smaller change as it was already less saline.

The falls in alkalinity and conductivity, and increased transparency (Figure 4.2) were linked to rain-induced dilution of lake water from catchment rainfall. These effects follow small opposite effects due to inflow of sediment-bearing river water within a few days of rainfall events. Mean fractions of inorganic carbon were calculated for sites CI, MR and the Main Lake (Table 4.4) which shows bicarbonate ions were the dominant form of inorganic carbon. A significant difference in pH occurred between site MR and both CI ($p = 0.007$) and Main Lake ($p = 0.016$) but no such difference between site CI and the Main Lake ($p = 0.08$). For all combinations, differences in mean alkalinity are highly significant ($p < 0.001$) as there is much less variation in data. Neither

measurement shows a significant difference between sections of the Main Lake. Background chemistry shows some differences between sites as detailed in Table 4.5. Site CI showed lower concentrations of silicate than sites MR ($p = 0.022$) and the Main Lake ($p = 0.014$). Sulphate concentrations were similarly higher at Site MR than CI ($p = 0.007$) and the Main Lake ($p = 0.001$). Site MR also showed significantly higher fluoride concentrations ($p = 0.020$) than the Main Lake. Sodium and potassium levels were only measured twice, therefore they can not be compared statistically, but provide an indication of background conditions.

Chloride concentrations at different sites showed no significant differences and were generally correlated with high coefficients ($C_p = 0.904$ to 0.929) although these are non-significant due to the small number of degrees of freedom.

Table 4.4 Concentrations of inorganic carbon fractions.

Fraction	Concentration (mM)		
	Site CI	Site MR	Main Lake
Total CO ₂	1.49	1.20	1.28
Free CO ₂	0.01	0.03	0.01
HCO ₃ ⁻	1.46	1.19	1.25
CO ₃ ²⁻	0.02	0.01	0.01
OH ⁻	≈ 0	≈ 0	≈ 0
Alkalinity (mg/l as CaCO ₃)	151.00	119.70	127.88
pH	8.55	7.93	8.29

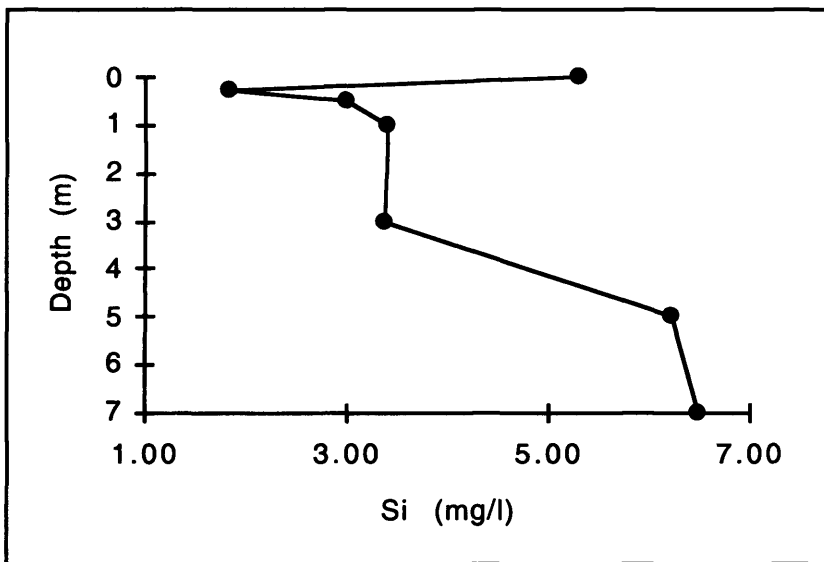
For CI and MR, $n = 11$; for the Main Lake, $n = 38$

Table 4.5 Concentrations of background chemical ions.

Site	Mean surface ionic concentration (mg/l)					
	Si	SO ₄ ²⁻	Cl ⁻	F ⁻	Na ⁺	K ⁺
CI	5.3	10.4	19.0	1.43	6.9	1.0
MR	11.3	20.1	18.4	1.55	9.7	0.9
Main	11.3	11.2	15.8	1.38	8.2	1.3

Silicate concentrations were least strongly correlated between sites ($C_p = -0.213$ to 0.186) and also showed variations with depth. This is illustrated by Figure 4.3 which shows the silicate depth profile for site CI (other sites were not profiled). As primary production was maximal at 0.5 - 1m, silicate concentrations were lowest at this depth, being negatively correlated with productivity ($C_p = -0.698$, $df = 5$) although this is non-significant for mean values. Silicate profiles (section 4.1.6) show that depletion is not limiting.

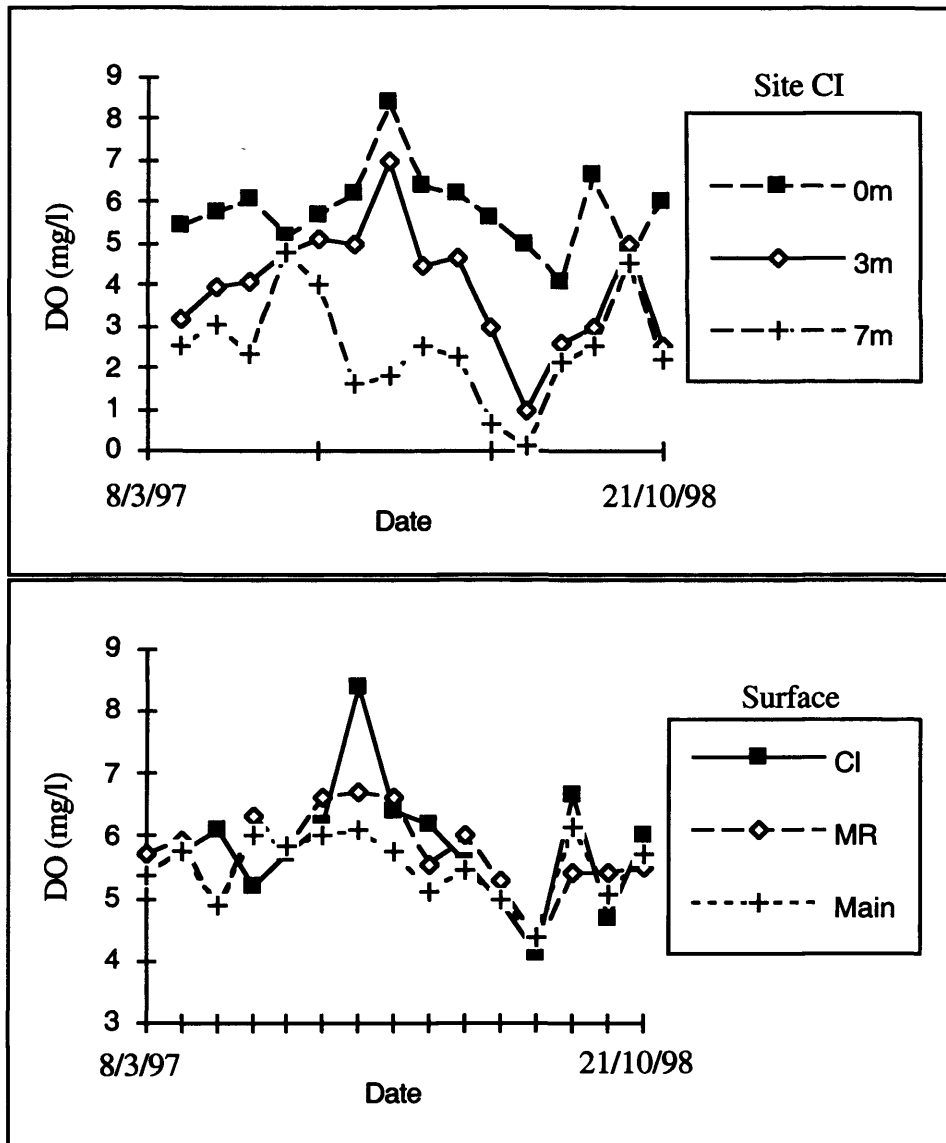
Figure 4.3 Silicate profile for Site CI.



DO levels were significantly correlated for all 3 sites (Figure 4.4), whilst only Main lake and CI were correlated significantly when considering oxygen change with depth (although this may be due to the low number of degrees of freedom). In summary;

Dissolved oxygen	CI & MR	$C_p = 0.968$	$df = 3$	$p < 0.01$
	Main & MR	$C_p = 0.928$	$df = 3$	$p < 0.05$
	Main & CI	$C_p = 0.984$	$df = 6$	$p < 0.001$
Oxygen change	CI & MR	$C_p = 0.770$	$df = 3$	$p > 0.1$
	Main & MR	$C_p = 0.843$	$df = 3$	$p > 0.05$
	Main & CI	$C_p = 0.926$	$df = 6$	$p < 0.001$

Figure 4.4 Dissolved oxygen changes 8/3/97 - 21/10/98.



Dissolved oxygen levels for all sites were significantly different ($p < 0.001$) between epilimnetic and hypolimnetic water with site CI showing the greatest difference and site MR the least. This was due to the less complete mixing found at the deeper, relatively sheltered site CI, and thus the 7m sample showed a slightly different pattern of variation to the other depths measured. As illustrated in Figure 4.5, there was no significant difference between DO levels for different sites at depths shallower than 3m ($p = 0.083$ to 0.806). At 5m depth however the oxygen concentration at site CI was significantly lower than that of Main lake ($p = 0.001$). Below this point, site CI became progressively more deoxygenated as incomplete mixing occurred.

Figure 4.5 Dissolved oxygen profiles with surface 1m magnified.

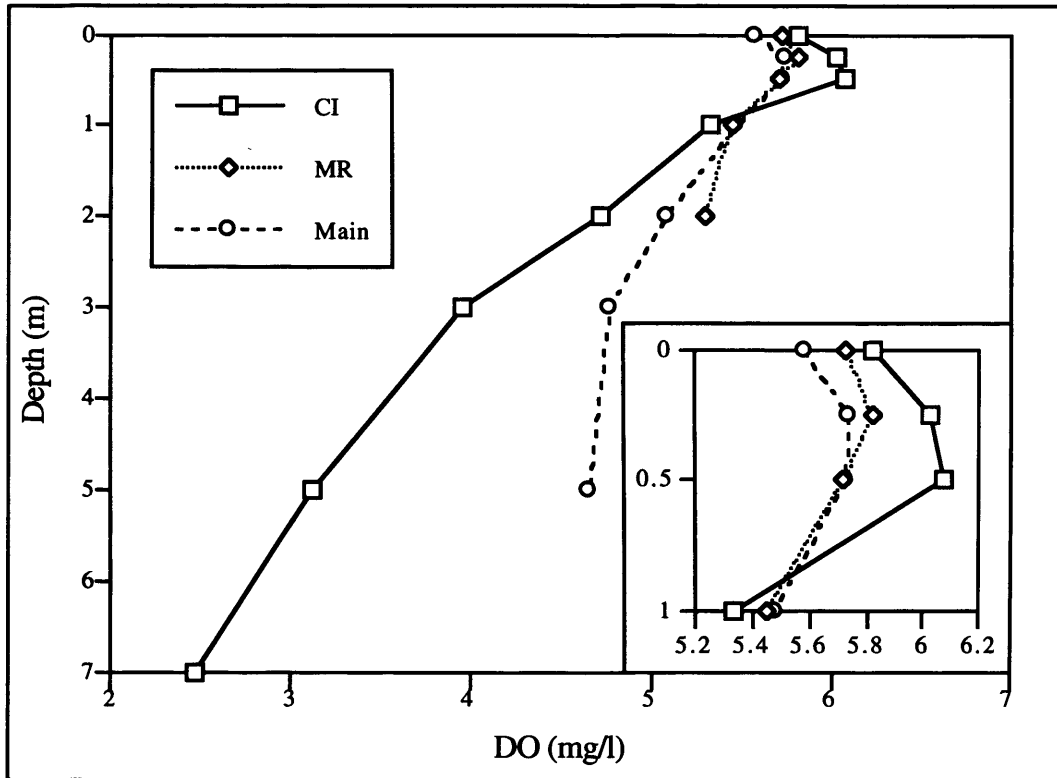


Figure 4.6 Profiles of dissolved oxygen change.

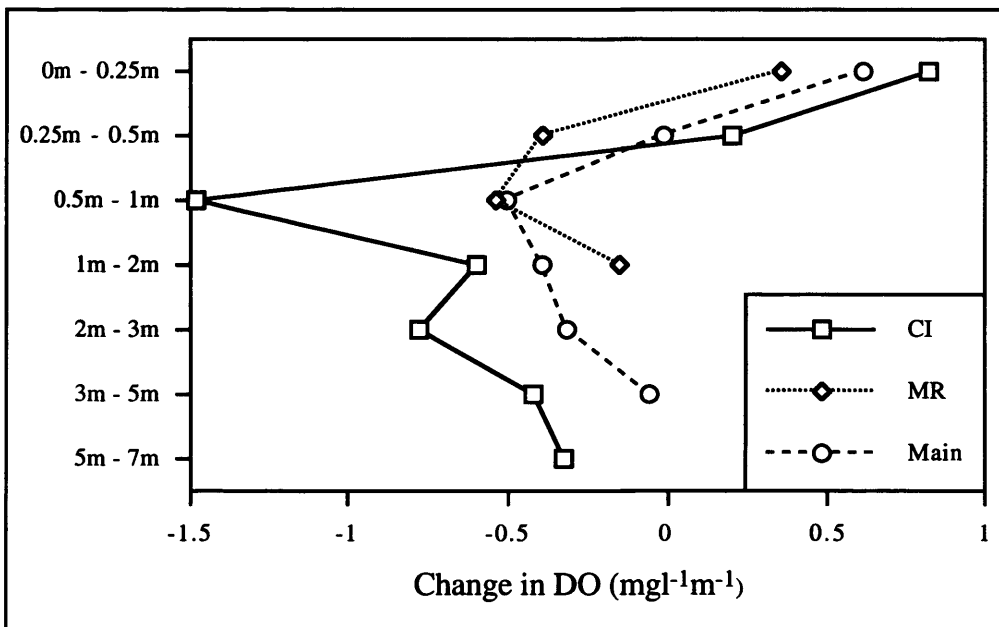


Figure 4.6 shows the greatest change to be within the 0.5 - 1m section for all sites and thus is the location of any oxycline produced through temporary stratification. There was no significant difference in DO change with depth between MR and Main lake ($p >$

0.05), whilst CI showed a significantly different level of change ($p < 0.01$) from both these sites. Temperature measurements however do not provide such a clear picture of stratification. Sites CI, MR and the Main lake showed mean temperature reduction over the entire profile of 0.67°C , 0.33°C and 0.62°C respectively, but this is not closely related to the oxycline between 0.5m and 1m depth. For the same sites, this section is responsible for only 12.5%, 25.00% and 24.53% of mean temperature reduction respectively as it is spread more evenly over depth than dissolved oxygen reduction. It is therefore generally difficult to detect a definite thermocline, especially as only a small thermal gradient is required in the tropics. Nutrient measurements from site CI indicated that nutrients were recycled in the water column as well as released from sediments under anaerobic conditions, as there was not complete epilimnetic depletion during stratification. Site CI also generally had the lowest chlorophyll *a* concentration although diatoms were sometimes numerous.

Table 4.6 Inter-site comparison of some background conditions. Italics indicate non-significant correlation. All comparisons by t-test show significant differences between sites ($p < 0.05$) except Conductivity for site MR and the main lake.

C_p (prob.)	Alkalinity (df = 8)	Conductivity (df = 14)	Transparency (df = 14)
Main vs CI	0.959 (< 0.001)	<i>0.398 (> 0.1)</i>	<i>0.227 (> 0.1)</i>
Main vs MR	0.971 (< 0.001)	0.793 (< 0.001)	<i>0.092 (> 0.1)</i>
CI vs MR	0.927 (< 0.001)	0.719 (< 0.01)	0.852 (< 0.001)

For these parameters, sites are therefore different but closely correlated. These data show MR to be a source of fresh water whilst CI remains partially hydrologically separated from the Main Lake.

4.1.3 Nutrient levels

In Table 4.7, the only combination of depths at site CI giving a significant difference between SRP concentrations is 0m and 7m ($p < 0.001$). SRP concentrations at 0m & 3m and 0m & 7m are also not correlated ($C_p = 0.149$ & -0.086 respectively; $df = 10$, $p > 0.1$) indicating that different processes govern SRP fluctuations in the epilimnion and

hypolimnion. Within the hypolimnion therefore, SRP concentrations at 3m & 7m are both significantly greater with depth ($p = 0.003$) and strongly correlated ($C_p = 0.927$, $df = 12$, $p < 0.001$) indicating constancy of processes within a stable layer. Concentrations between different depths within mixed layers were not correlated however, either for epilimnetic water or samples within unstratified sections of the water column. The zero values for nitrate, ammonium and SRP show that nutrients are most likely to be depleted and limiting at 0.5m depth where productivity is approximately maximal.

Table 4.7 Nutrient profiles of nitrogen and phosphorus fractions.

$\mu\text{M NH}_4^+$				$\mu\text{M SRP}$		
Depth (m)	CI	MR	Main lake	CI	MR	Main lake
0	0.08	0.13	0.08	0.08	0.12	0.07
0.25	0.01	0.04	0.05	0.05	0.05	0.07
0.5	0.00	0.06	0.01	0.00	0.02	0.03
1	0.01	0.12	0.04	0.01	0.11	0.17
2	-	0.17	0.14	-	0.18	0.17
3	0.22		0.13	0.12		0.13
5	-		0.16	0.21		0.13
7	0.73			0.37		

$\mu\text{M TN}$				$\mu\text{M TP}$		
Depth (m)	CI	MR	Main lake	CI	MR	Main lake
0	2.56	7.17	2.37	0.16	0.19	0.14
0.5	3.05	-	-	0.13	-	-
1	2.61	9.10	2.55	0.13	0.26	0.11
2	-	8.64	2.14	-	0.31	0.11
3	2.54		2.91	0.24		0.18
5	-		2.85	-		0.20
7	4.09			0.75		

$\mu\text{M NO}_3^-$			
Depth (m)	CI	MR	Main lake
0	0.07	0.10	0.08
0.25	0.04	0.05	0.03
0.5	0.00	0.06	0.04
1	0.04	0.14	0.05
2	-	0.19	0.10
3	0.25		0.14
5	-		0.14
7	0.99		

A significant increase in SRP with depth occurred comparing site OW at 0m and 3m ($p = 0.012$) but no significant correlation ($C_p = 0.316$, $df = 5$, $p > 0.1$). Comparing values for 0m and 1m within the site CI epilimnion gives a significant decrease with depth ($p = 0.004$) and again no significant correlation ($C_p = -0.058$, $df = 12$, $p > 0.1$). This

indicates that there are processes causing variations in conditions both between and within layers. Figure 4.7 thus shows the different relationships between dissolved oxygen and SRP concentrations for permanently mixed (Main Lake) and temporarily stratified (Site CI) conditions. The Main Lake showed a steady, unstratified reduction in DO with depth of approximately 0.2 mg/l/m, apart from a small increase of 0.2 mg/l at 0.5m where there is the greatest rate of primary productivity. Similarly there was little increase in SRP with depth, with almost complete depletion at 0.5m. In contrast, Site CI showed a more rapid reduction in DO with depth (0.5 mg/l/m) although surface levels and the peak at 0.5m were similar to those measured in the Main Lake. The low hypolimnetic oxygen levels, which were sometimes below 1.0 mg/l, may however allow phosphorus release from sediments as illustrated by the increase in SRP levels below 3m, although above this depth both sites show similar concentrations.

Figure 4.7 Oxygen and SRP profiles.

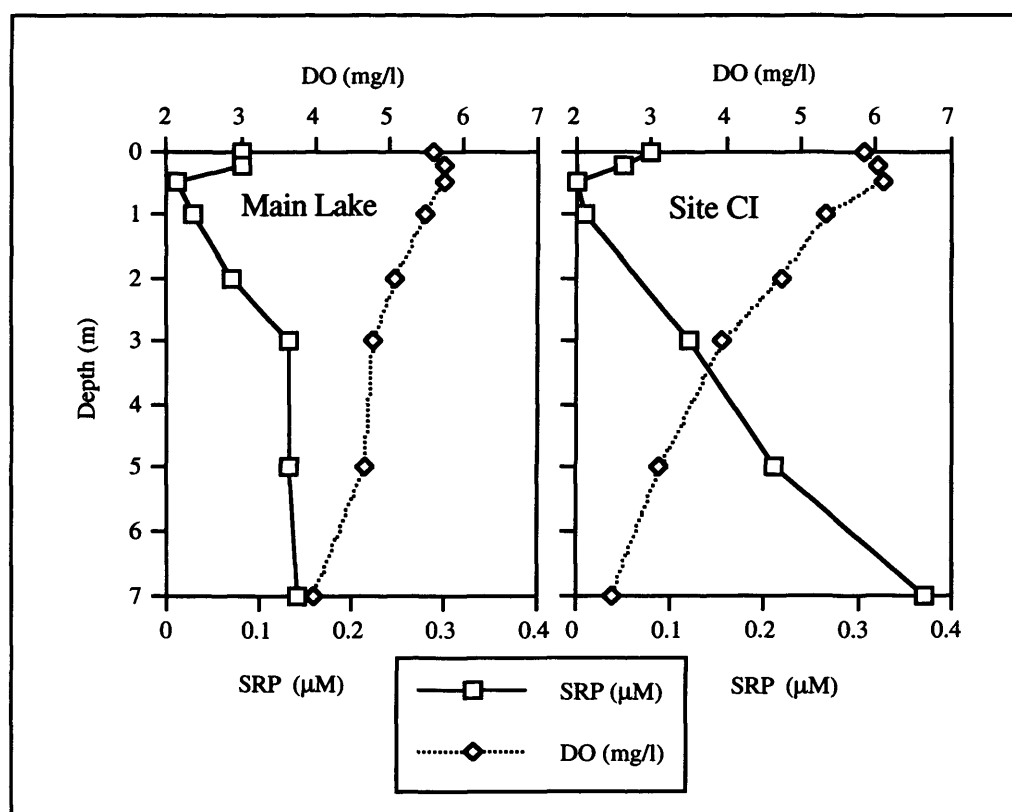


Table 4.8 shows correlations between a range of chemical and physical factors. Conductivity was not correlated with any nutrient fractions as they are not linked directly with levels of dissolved solids. Secchi depth was negatively correlated with

ammonium, SRP and especially TN concentrations. The processes which increased nutrient levels therefore also reduced transparency. This was not simply due to inflow of sediments, as Secchi depth was most poorly related to TP, despite phosphorus being transported in particulate-bound form.

Table 4.8 Correlations between chemical and physical factors.

Factor	Correlation (probability)				
	NO ₃ ⁻	NH ₄ ⁺	TN	SRP	TP
Secchi	-0.205 (> 0.1)	-0.393 (p < 0.01)	-0.486 (p < 0.001)	-0.33 (p < 0.01)	-0.034 (p > 0.1)
Cond.	0.102 (> 0.1)	-0.164 (> 0.1)	-0.196 (> 0.1)	0.071 (> 0.1)	-0.171 (> 0.1)
NH ₄ ⁺	0.912 (p < 0.001)				
TN	0.224 (p < 0.05)	0.236 (p < 0.02)			
SRP	0.708 (p < 0.001)	0.715 (p < 0.001)	0.457 (p < 0.001)		
TP	0.826 (p < 0.001)	0.781 (p < 0.001)	0.324 (p < 0.001)	0.839 (p < 0.001)	

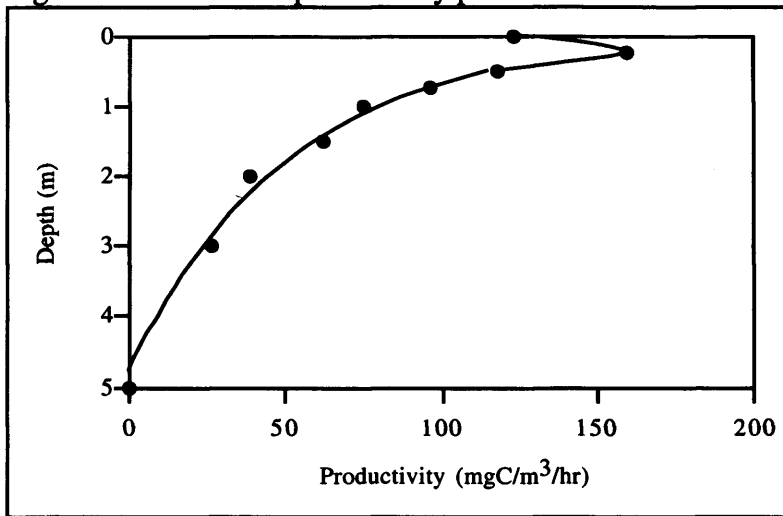
For Secchi and conductivity correlated with nutrient fractions, df = 64

For Secchi and conductivity correlated with total nutrients, df = 52

For all nutrient correlations, 147 ≤ df ≤ 238.

All combinations of nutrient fractions were significantly correlated as similar processes affected their concentrations such as nutrient inflow, algal use and accumulation at depth. TN however did not correlate as closely with nitrogen fractions as with phosphorus fractions because it is not easily transformed into these ions. Secchi depth and conductivity were also not significantly correlated ($C_p = 0.242$, df = 64, $p > 0.05$), indicating little effect of dissolved solids on transparency, whilst water temperature and pH were negatively correlated ($C_p = -0.275$, df = 72, $p < 0.02$). This latter result is a standard response as pH is expected to fall by approximately 0.01 per 1°C rise in temperature (Mackereth *et al* 1989); in fact, this correlation gives a pH response of -0.08 per 1°C rise in temperature. Comparing conductivity values for the inflowing rivers, all pairs showed significant differences ($p \approx 0$) using Chi² testing. For total suspended solids (TSS), there were no such differences.

Figure 4.9 Main Lake productivity profile.

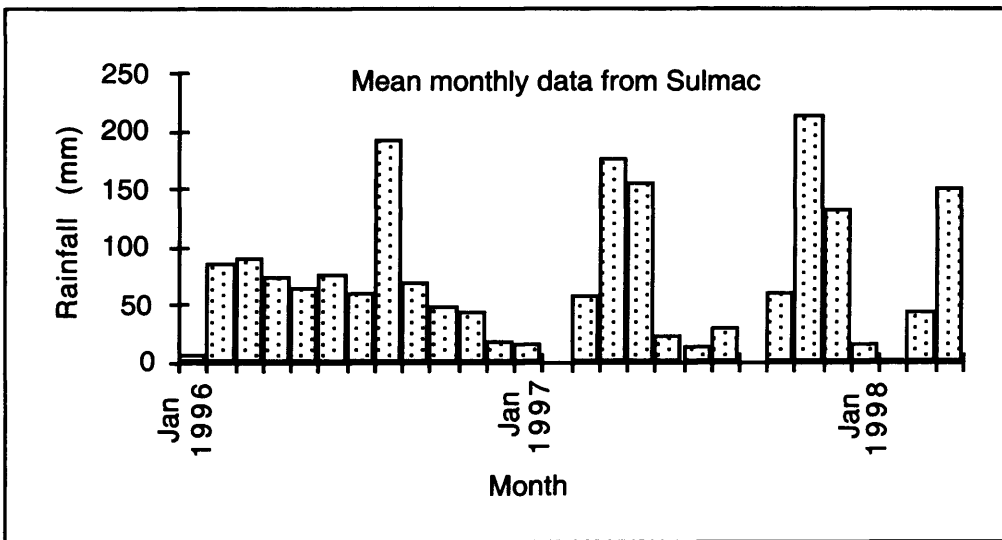
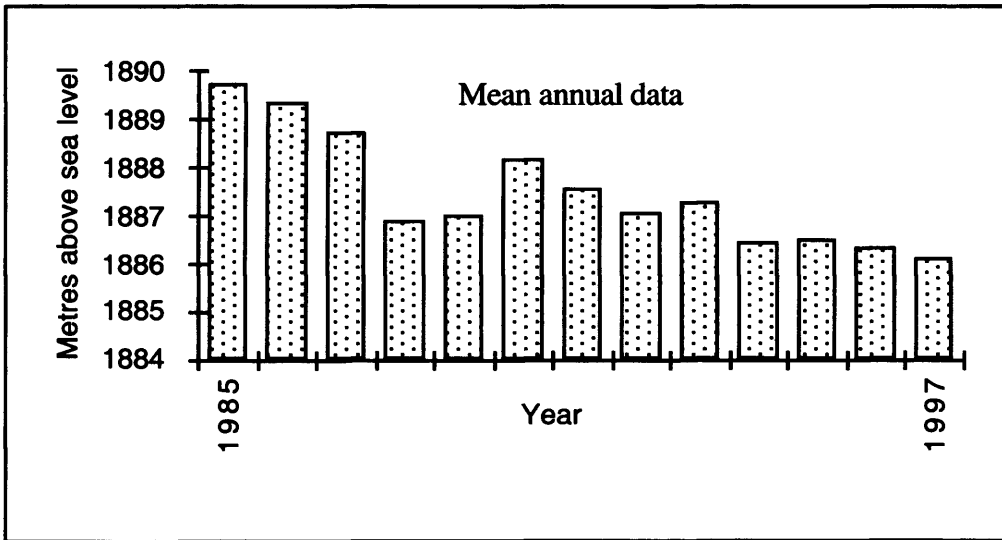
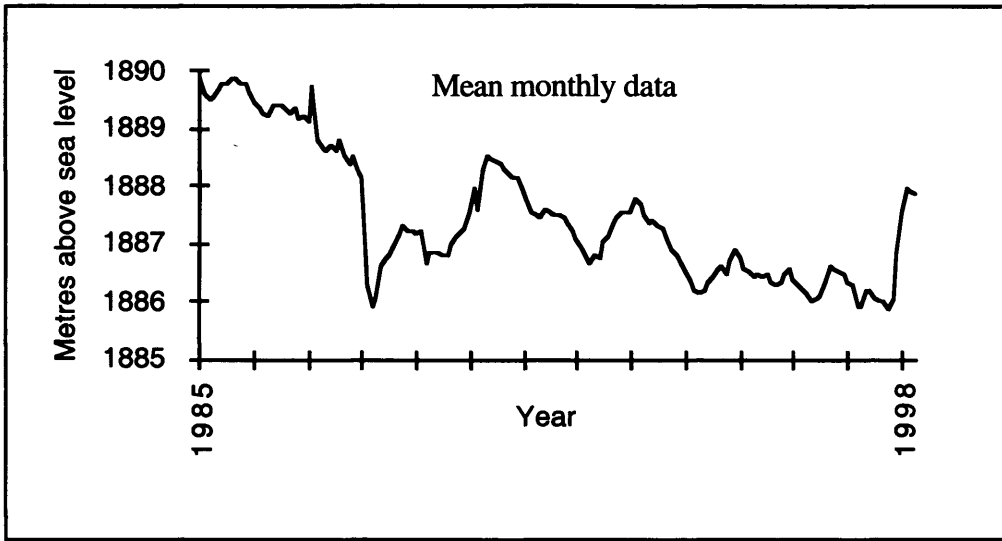


4.1.5 Climatic factors

In the tropics there is no seasonality compared with temperate zones, although Kenya experiences a bimodal monsoon-driven system. Tropical seasonality is thus defined by the patterns of change seen in climatic parameters, usually rainfall. Work by Vincent *et al* (1979) explains the climatic system driving rainfall patterns in East Africa which in turn influence lake levels. In August, moist westerly winds of the extensive West African circulation system occur down to an altitude of 2 - 3 km and induce a single August rainfall peak in the Kenyan highlands. The rest of the region experiences rainfall peaks in April/May and November related to the north-south passage of the Intertropical Convergence Zone (ITCZ). Lower altitudes experience drier south-easterly Trade winds. Lake Naivasha's inflow is dominated by rainfall in the Nyandarua Mountains, with a precipitation regime which disturbs the ITCZ and prolongs rains. Rainfall peaks at approximately 2500m altitude with maxima on the SE slopes. There is no correlation between local rainfall and Naivasha lake level, but highland rainfall (July - September) is highly correlated ($p < 0.1$) with lake level changes in September. Annual rainfall over East Africa, and its seasonal distribution are therefore related to changes in larger-scale tropical systems. Lake levels are correlated with global tropical parameters but different lakes may respond to different aspects of the same large-scale system. For instance, Lake Naivasha's level is negatively correlated with the strength of the North Atlantic

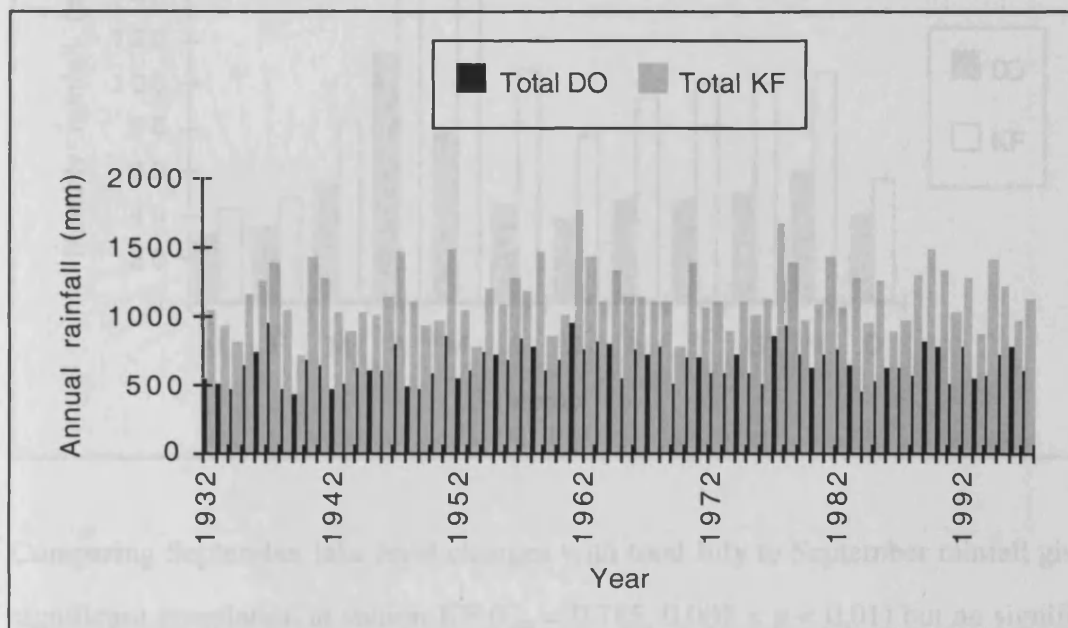
circulation (coeff = -0.33, $p < 0.2$) whilst that of Lake Victoria shows a positive correlation (coeff = 0.32, $p < 0.2$). Lake Naivasha experiences its main level increases in May and September with over 85% of level variance due to long-term (> 20 year) oscillations. At Lake Victoria rises occur mostly in May with some lesser ones in December, and most variation in the shorter-term. This is because level fluctuations in Lake Victoria correspond to the bimodal rainfall system whilst changes at Lake Naivasha indicate varying penetration of moist West African air. Level changes of these two lakes therefore show little similarity although they may be driven by planetary processes. Figure 4.10 illustrates lake level and local rainfall data for Lake Naivasha. In 1996, neither the long April-May rains nor the short November rains arrived, causing drought conditions, although there had been a peak of unseasonal rain in August. In 1997, rainfall followed its bimodal pattern more closely until November when instead of the usual short rains, the El Niño phenomenon brought rains which continued several months into 1998 (apart from a relatively dry period in February). These events caused flooding throughout Kenya, but in the Naivasha area the effects were less serious and resulted in the lake level rise mentioned above. This rise was the largest and most rapid since the mid-1970s. After the cessation of El Niño rains a dry period commenced in late 1998 as the short rains failed, with resumption of drought conditions. Lake level and local mean monthly rainfall at Sulmac are not generally correlated, although periods of particularly high rainfall are followed by rises in lake level. In early 1998, site HP was 8m deep, with the main basin 6-6.5m deep gradually falling to 4-4.5m depth at site RI and 2-2.5m depth at site MR. The centre of Crescent Island lagoon was 18m deep. During the rest of the study, the lake was approximately 1.5-2m shallower, although site MR tended to move as fluctuating lake level changed the location of the river mouth and was always around 2m deep. These figures equate approximately with the lake level immediately prior to its rapid decrease in January 1988 whilst mean annual data still suggests a downward trend since records began in 1908. There have been a number of large (> 2m) fluctuations associated with major droughts or rainfall events, and no regular periodicity is seen.

Figure 4.10 Naivasha lake level and local rainfall 1985 to 1998.



Using monthly rainfall data from weather stations at Naivasha District Office (DO) and Kinangop Forest (KF) provides a comparison between lakeside and upland climatic conditions respectively. The stations are approximately 15 km apart with a 600 m difference in altitude. Station DO is situated at approximately 1900 m above sea level, whilst Station KF is at approximately 2500 m above sea level, and therefore experiences the greatest rainfall. Throughout the 66-year period 1932 to 1997 inclusive, mean annual rainfall at station DO was 643.1 mm (s.d. = 130.2 mm, minimum = 417.2 mm, maximum = 941.9 mm) and at station KF 1129.8 mm (s.d. = 220.56 mm, minimum = 711.0 mm, maximum = 1765.9 mm). Upland rainfall is significantly greater than at the lakeside ($p < 0.001$, $n = 66$) and neither station shows a trend in rainfall over this period (Figure 4.11).

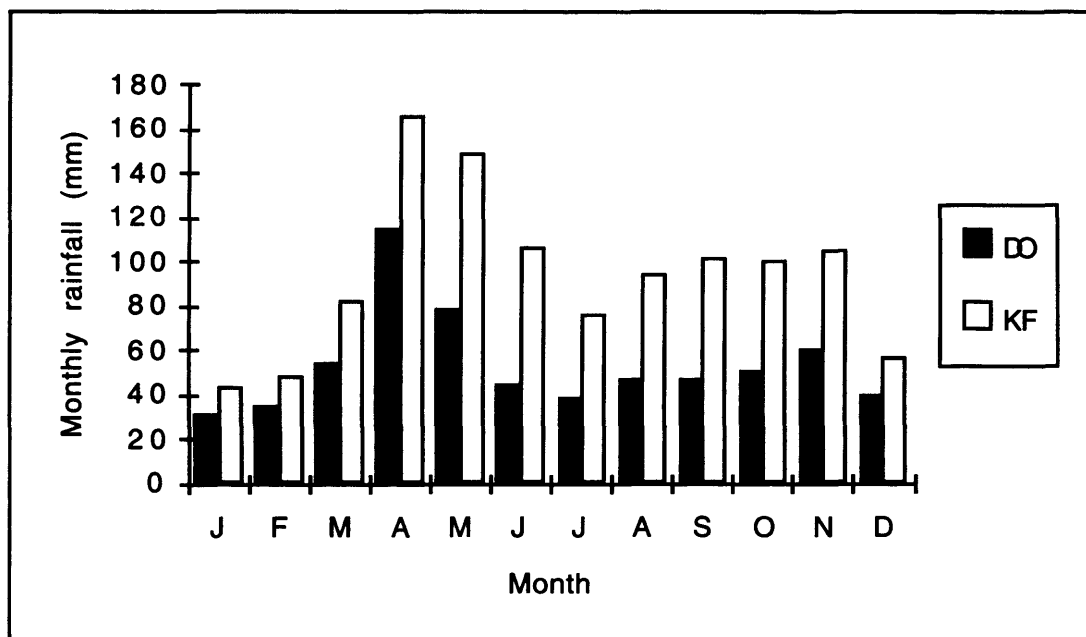
Figure 4.11 Total annual rainfall at two weather stations in the Naivasha catchment, lakeside at DO (District Office) and upland at KF (Kinangop Forest), 1932 to 1997.



Rainfall between stations is highly correlated for both monthly ($C_p = 0.694$, $p < 0.001$) and annual ($C_p = 0.680$, $p < 0.001$) data. For both stations the wettest year was 1961 and the driest year was 1939. None of the next 9 wettest and driest years match between stations, indicating that although there is close correlation between sites, extreme events or periods may be localised.

In the 13-year period 1985 to 1997 inclusive, there is no significant correlation between rain and lake level for either station for the same month ($p > 0.1$ for both stations). There is also no significant correlation between rain and lake level one, two or three months later ($p > 0.1$ for both stations and all months). These correlations allow for the time lag required for rainwater to be transported from the catchment to rivers, and then to flow into the lake. A bimodal seasonal pattern is seen for rainfall at both stations with the major peak in April and May corresponding with the long rains, and a minor peak in November corresponding with the short rains (Figure 4.12).

Figure 4.12 Monthly rainfall at two weather stations in the Naivasha catchment, lakeside at DO (District Office) and upland at KF (Kinangop Forest).



Comparing September lake level changes with total July to September rainfall gives a significant correlation at station KF ($C_p = 0.785$, $0.001 < p < 0.01$) but no significant correlation for station DO ($C_p = 0.511$, $p > 0.05$) for the period 1985 to 1997 inclusive. This is in contrast with the comparisons detailed above between all lake level and rainfall data, which show no such relationship.

Figure 4.13 Prevailing ground level wind direction over Lake Naivasha.

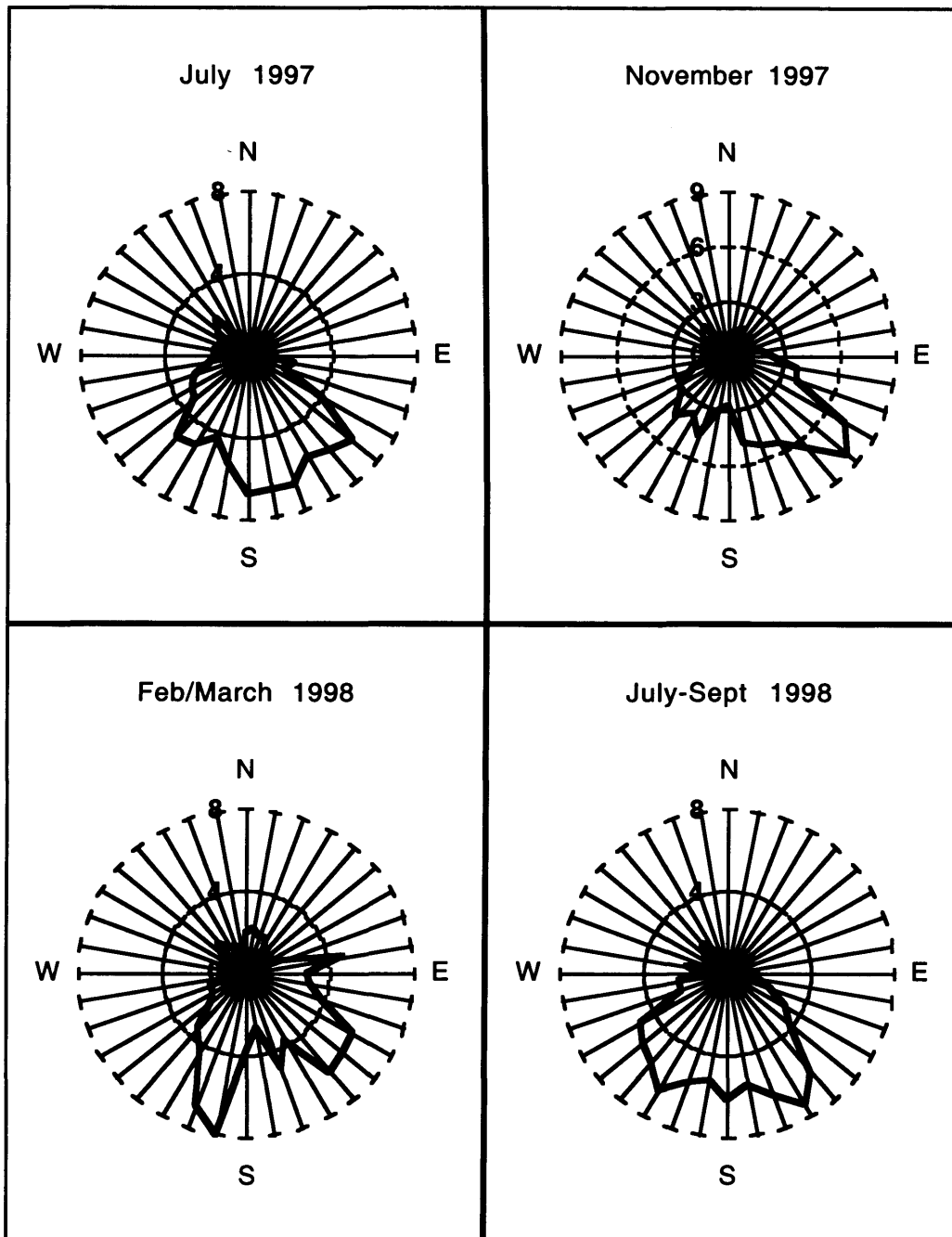


Figure 4.13 illustrates the change in prevailing wind direction over a period of 15 months, with the radial scale indicating the % of time wind comes from a given direction. Wind is south-westerly to easterly throughout the year, becoming more south-easterly during periods of rain. The November 1997 diagram shows the onset of El Niño rains with prevalent SE winds bringing rain from the Indian Ocean. The Feb/March 1998 diagram shows more SSW winds with little rain during this period.

Figure 4.14 Peak daily ISR July to September 1998.

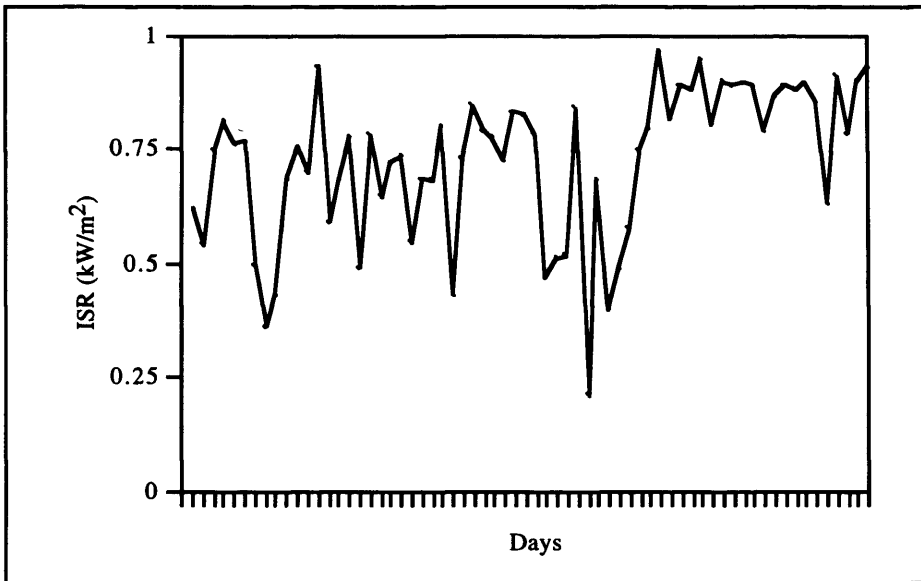


Figure 4.14 illustrates an example of variation in daily peak ISR over a period of approximately two months. Variations are largely due to cloud cover, as seen from the negative relationship between rainfall and ISR ($C_p = -0.550$, $p < 0.001$). This indicates how climatic parameters may be closely linked. For instance, pressure and wind speed are positively related ($C_p = 0.300$, $p < 0.01$), whereas wind speed is independent of wind direction, showing no significant differences between directions. ISR is also negatively correlated with relative humidity ($C_p = -0.641$, $p < 0.001$), as intense insolation dries the air. This has implications for evaporation, and hence water loss from the lake, which is increased by lower humidity. Figure 4.15 shows variations in peak daily atmospheric pressure for three separate periods. Daily variations are greater than monthly fluctuations and over longer periods, no trend was found in atmospheric pressure. No relationship was found between pressure and productivity ($C_p = 0.090$, $p > 0.2$), although pressure is related to wind speed which in turn drives mixing and breaks temporary stratification. Figure 4.16 illustrates examples of the daily cycle of climatic factors with wind speed increasing in the afternoon to a peak before falling overnight, following the same pattern of atmospheric pressure.

Figure 4.15 Peak daily atmospheric pressure July 1997 to February 1998.

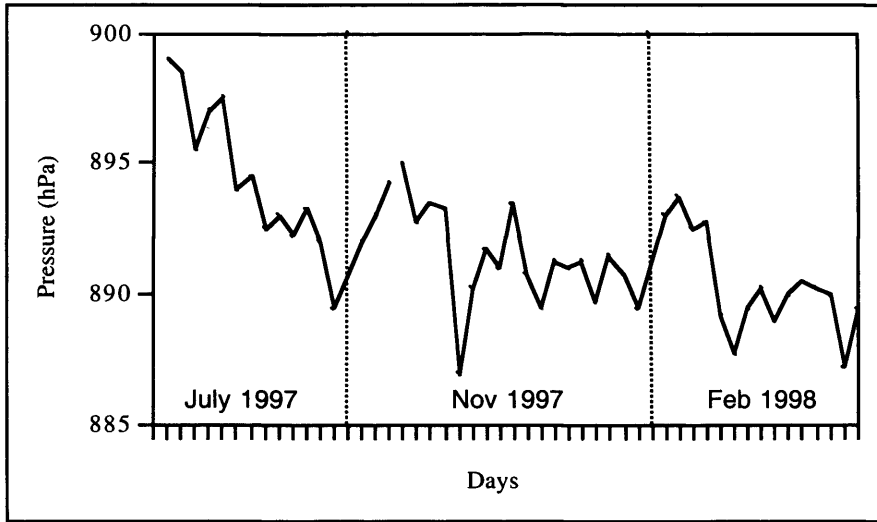
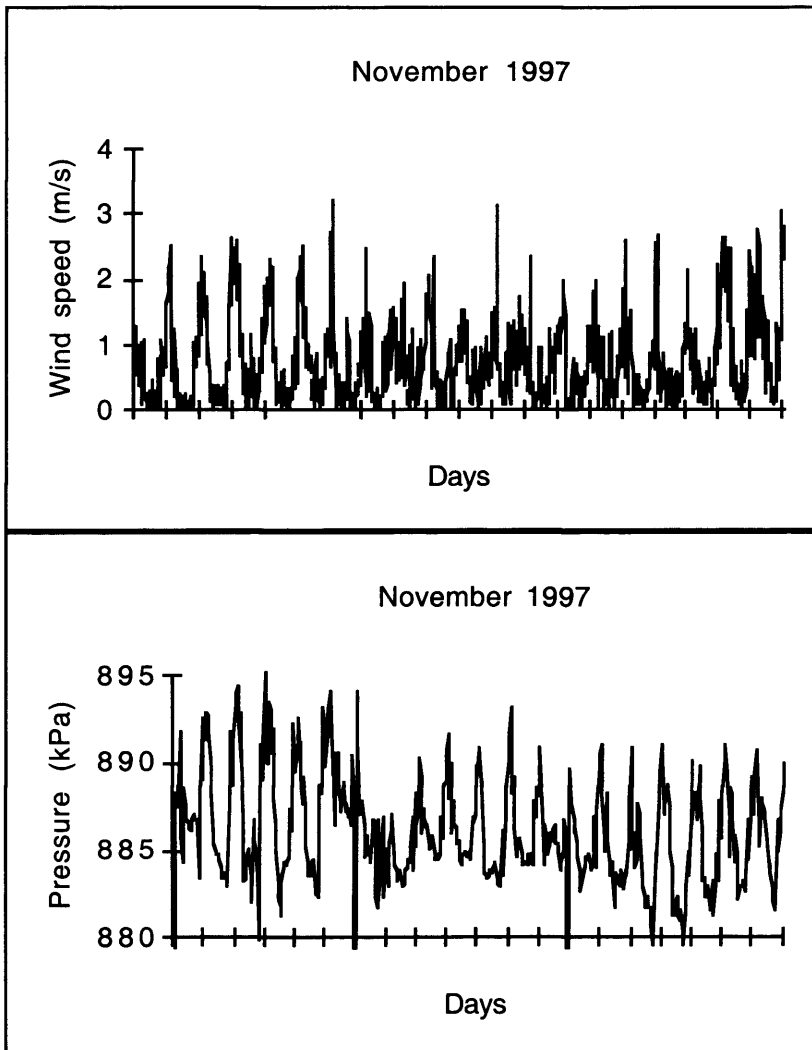


Figure 4.16 Daily cycles of wind speed and atmospheric pressure.



4.1.6 Nutrient dynamics

The main source of allochthonous materials is the River Malewa which shows a number of peaks in sediment and nutrient load. This was most easily seen with the onset of El Niño rains between October and November 1997. This caused large increases in TSS, particulate phosphorus (PP), TP and TN at various distances downstream as indicated by bold type in Table 4.9. These increases were largely between 2.5 and 35.5 km downstream. Similar peaks were seen during October and November in the rivers Gilgil and Karati. Differences in TSS between rivers (both at source and 30km downstream) and over time were investigated using Chi² tests. This indicates no significant difference in TSS levels between rivers, although the River Malewa has much greater flow therefore its absolute contribution of TSS to Lake Naivasha is proportionally larger. There were however differences over time related to differences between high and low rainfall periods.

Table 4.9 Changes in sediment and nutrient transport in the River Malewa with the onset of 1997 El Niño rains.

km	TSS (mg/l)			PP (µM)		
	Oct	Nov	% change	Oct	Nov	% change
-5	0.03	0.02	-33.33	2.48	2.32	-6.45
0	0.25	0.18	-28.00	5.45	5.28	-3.12
2.5	0.06	0.23	283.33	3.09	11.16	261.17
10.5	0.073	0.21	187.67	3.53	10.12	186.69
30.5	0.0533	0.32	500.38	2.98	9.64	223.49
35.5	0.0267	0.325	1117.23	2.73	9.38	243.59
68	0.056	0.03	-46.43	2.65	1.36	-48.68
km	TP (µM)			TN (µM)		
	Oct	Nov	% change	Oct	Nov	% change
-5	2.54	2.64	3.94	47.85	31.05	-35.11
0	6.46	6.55	1.39	23.33	166.7	614.53
2.5	4.22	11.61	175.12	12.78	67.92	431.46
10.5	4.53	10.58	133.55	23.7	50	110.97
30.5	3.85	10.14	163.38	19.44	52.22	168.62
35.5	3.49	10.14	190.54	44.17	50	13.20
68	3.41	4.14	21.41	10.83	20.83	92.34

TSS was significantly correlated with TP ($C_p = 0.692$, $df = 38$, $p < 0.001$) and PP ($C_p = 0.715$, $df = 38$, $p < 0.001$), but not with TN ($C_p = 0.197$, $df = 26$, $p > 0.1$). P and

N values are however often correlated in the lake itself as factors affecting nutrient levels often influence a number of nutrient types through different processes. Calculating N:P ratios using TDN and SRP concentrations indicate whether nutrient limitation is nitrogen or phosphorus-based. TDN is taken to be the sum of nitrogen and ammonium concentrations as nitrite levels were negligible. Initial 1997 results are presented in Table 4.10.

Table 4.10 1997 nitrogen and phosphorus measurements.

Site	TDN (μM)	SRP (μM)	N:P ratio
CI	0.76	0.12	6.33
Main Lake	0.35	0.12	2.92
MR	1.04	0.26	4.00

An N:P ratio above 7.2 indicates possible P-limitation (Reynolds 1984) with a value above 10 strongly indicating nutrient stress. These data and all later monitoring values show the ecosystem to be primarily N-limited. Nutrient series as described in this section showed however that both types of limitation occur, although it was greater for nitrogen.

4.1.7 Nutrient series

For changes in nutrient levels during incubation, correlation coefficients were calculated for ' μM nutrient added' against 'changes in nutrient level (∂)' for both the total series and linear (sub-saturation) sections. These sections are investigated separately due to the logarithmic nature of the response of productivity to enrichment. This is due to a post-saturation plateau following the sub-saturated linear section. Correlating the series and response only up to this $1\mu\text{M}$ level thus produces clearer results. These are summarised in Table 4.11 for both absolute and % changes in SRP, NO_3 and NH_4 concentration within SRP, NO_3 and NH_4 enrichment series. The SRP series showed a strong correlation ($p < 0.01$) with ∂NO_3 and $\partial\%\text{NO}_3$ i.e. with increasing SRP there was a correspondingly greater reduction in NO_3 during incubation. SRP enrichment was not as significantly correlated with changes in NH_4 ($p < 0.05$) despite algal preference for ammonium over nitrate, although this apparent anomaly may just reflect low sample

number. Similarly, the ammonium series showed high correlation ($p < 0.01$) only with ∂ SRP and $\partial\%$ SRP as phosphorus limitation was increased through nitrogen enrichment. The nitrate series however only correlated with ∂ SRP at $p < 0.05$ significance, but was more strongly related ($p < 0.02$) to ∂ NH₄ and $\partial\%$ NH₄.

Table 4.11 Correlation of post-incubation changes in nutrient level with nutrient series.

C _p (probability)		Nutrient series (df total : df linear)		
Data correlated		SRP (5 : 3)	NO ₃ ⁻ (8 : 5)	NH ₄ ⁺ (8 : 5)
∂ SRP	Total	0.382 (> 0.1)	-0.268 (> 0.1)	-0.543 (> 0.1)
	Linear	-0.264 (> 0.1)	<i>-0.790 (< 0.05)</i>	-0.880 (< 0.01)
∂ %SRP	Total	0.685 (> 0.05)	0.559 (> 0.05)	-0.519 (> 0.1)
	Linear	0.765 (> 0.05)	0.434 (> 0.1)	-0.883 (< 0.01)
∂ NO ₃ ⁻	Total	-0.690 (> 0.05)	-0.225 (> 0.1)	0.603 (> 0.05)
	Linear	-0.965 (< 0.01)	-0.056 (> 0.1)	-0.332 (> 0.1)
∂ %NO ₃ ⁻	Total	-0.725 (> 0.05)	-0.169 (> 0.1)	0.550 (> 0.05)
	Linear	-0.965 (< 0.01)	-0.045 (> 0.1)	-0.511 (> 0.1)
∂ NH ₄ ⁺	Total	-0.555 (> 0.1)	-0.495 (> 0.1)	0.583 (> 0.05)
	Linear	<i>-0.918 (< 0.05)</i>	<i>-0.838 (< 0.02)</i>	-0.703 (> 0.05)
∂ %NH ₄ ⁺	Total	-0.537 (> 0.1)	-0.499 (> 0.1)	0.597 (> 0.05)
	Linear	<i>-0.914 (< 0.05)</i>	<i>-0.835 (< 0.02)</i>	0.637 (> 0.1)

Bold type indicates a significant correlation, however results giving $0.05 > p > 0.01$ (italics) are not considered sufficiently robust due to the number of correlations undertaken which suggest that such relationships may be by chance. Ammonium enrichment elicited the greatest productivity increase of the major nutrients in both absolute and % terms, productivity levels being significantly higher than series using nitrate (one-tailed $p = 0.001$), mixed nitrogen ($p = 0.007$) and SRP ($p = 0.003$). The mixed nitrogen and nitrate series did not produce significantly different responses ($p = 0.194$), whereas the response to SRP was significantly lower than both those of nitrate ($p = 0.005$) and mixed nitrogen ($p = 0.001$). Results are presented in Table 4.12 (italics indicate non-significance). All pairs of series were highly correlated and showed significantly different levels of productivity except for N and NO₃⁻. A similar form of response was seen for each series with a saturated productivity 'plateau' being reached at enrichments above a point between 0.8 and 1 μ M as illustrated in Figure 4.17. The

logarithmic responses showed good fit for all series with r^2 values ranging from 0.851 (mixed nitrogen) to 0.947 (SRP). SRP enrichment induced the lowest level of productivity due to Lake Naivasha being more limited by nitrogen than phosphorus. Ammonium elicited the greatest response due to algal preference for this over nitrate.

Table 4.12 Comparison of productivity responses to nutrient series.

	Correlation ($p < 0.001$ for all pairs)			
t-test prob.	SRP	N	NO ₃ ⁻	NH ₄ ⁺
SRP		≈ 1.000	0.990	0.995
N	0.001 (df = 6)		0.993	0.991
NO ₃ ⁻	0.005 (df = 6)	0.194 (df = 7)		0.996
NH ₄ ⁺	0.003 (df = 6)	0.007 (df = 7)	0.001 (df = 7)	

Figure 4.17 Response of productivity to nutrient enrichment series.

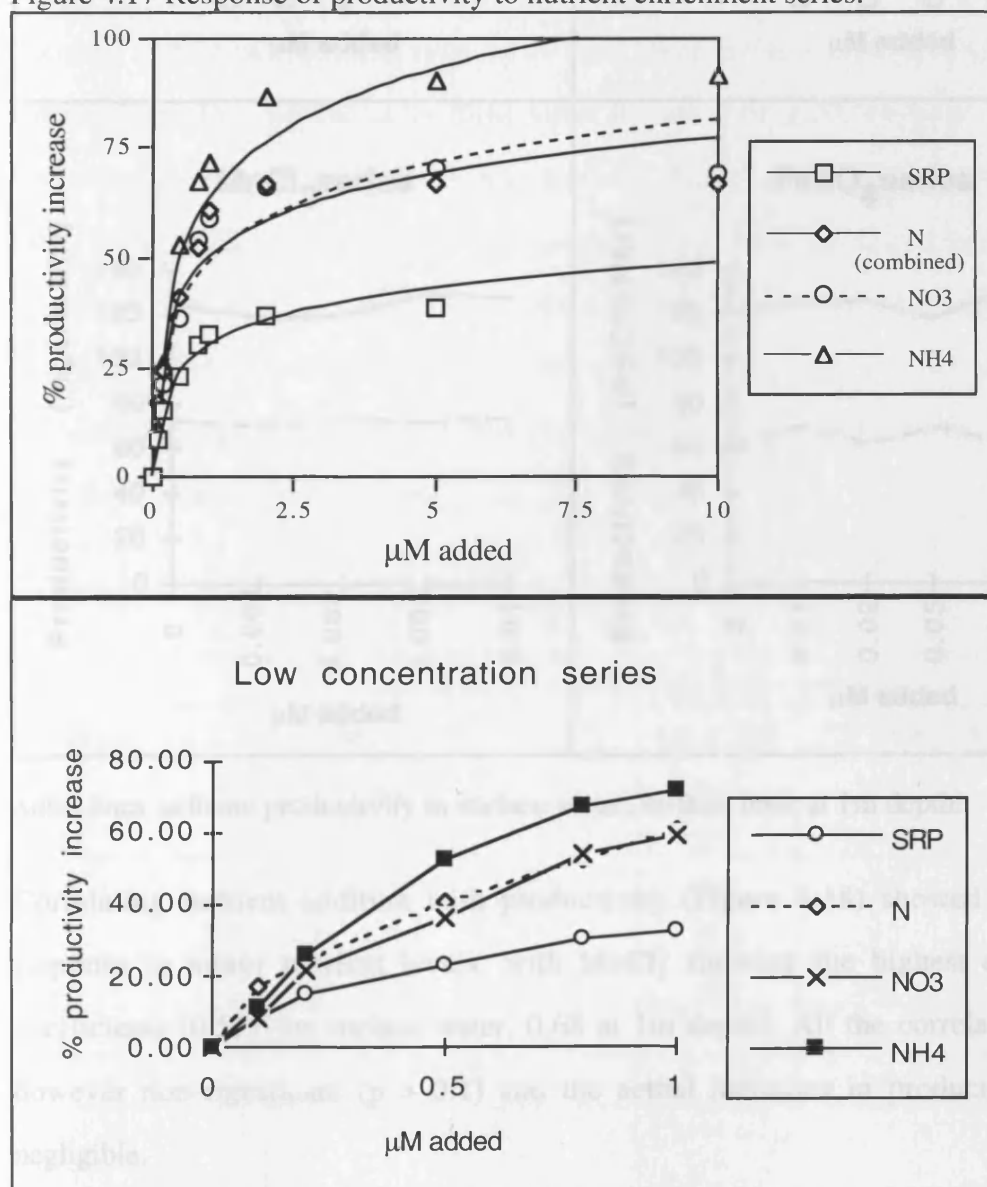
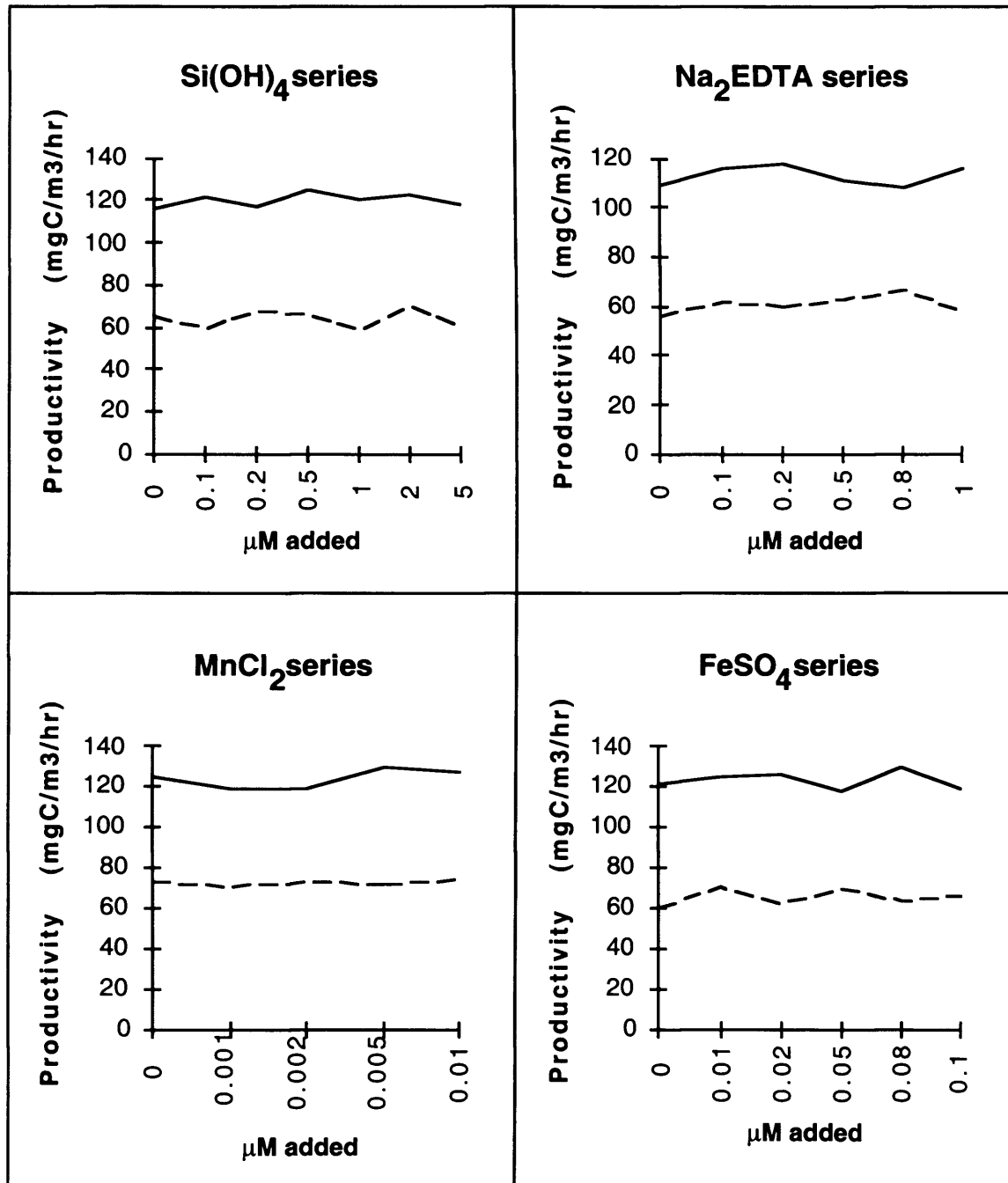


Figure 4.18 Response of primary productivity to enrichment of minor nutrients.



Solid lines indicate productivity in surface water, broken lines at 1m depth.

Correlating nutrient addition with productivity (Figure 4.18) showed no strong response to minor nutrient levels, with MnCl₂ showing the highest correlation coefficients (0.577 for surface water, 0.68 at 1m depth). All the correlations were however non-significant ($p > 0.1$) and the actual increases in productivity were negligible.

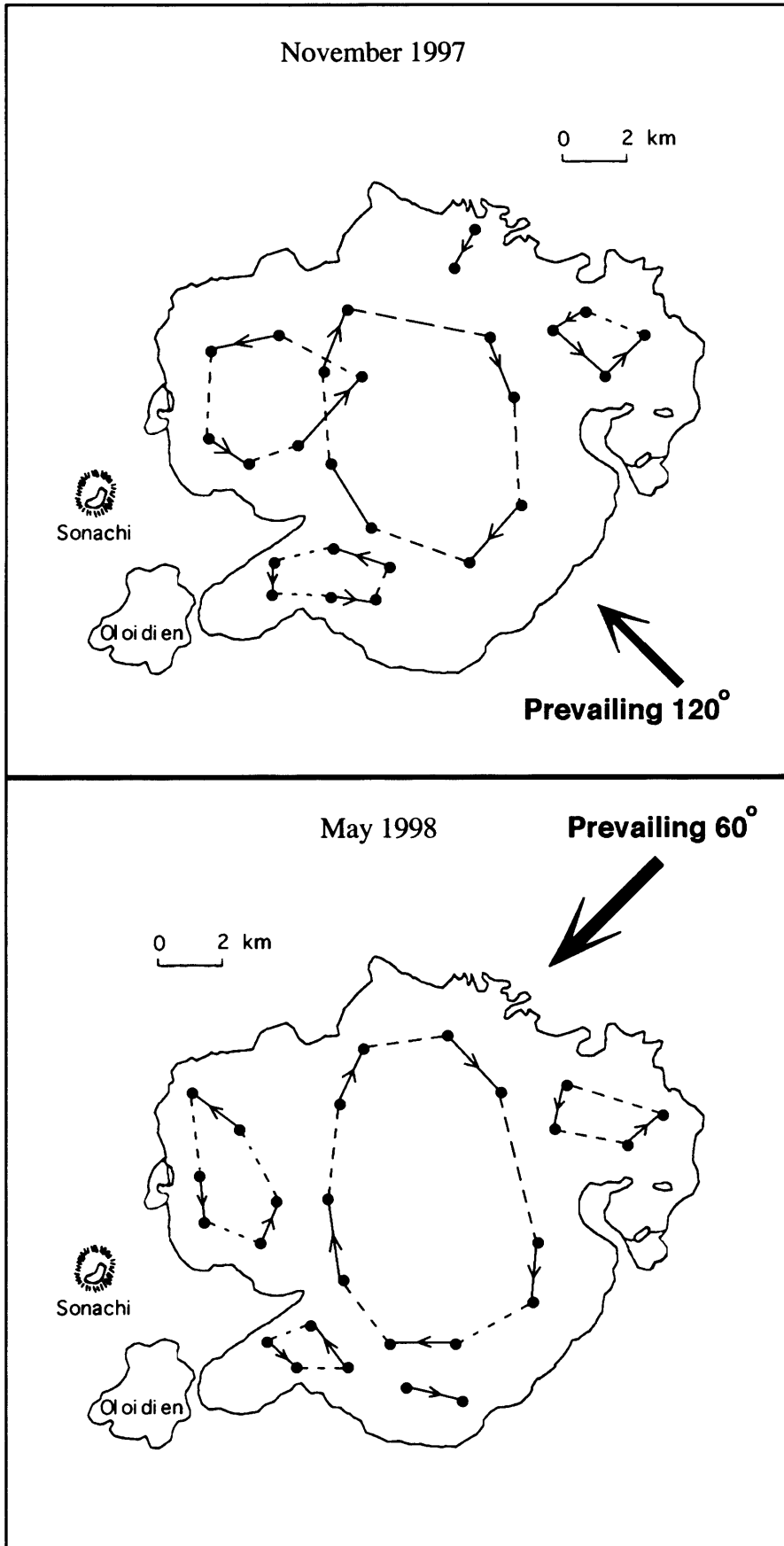
4.1.8 Nutrient transport and circulation

Circulation patterns for both months (in Figure 4.19) are similar, with solid lines indicating where the drogue was followed continuously and broken lines indicating where it was transported by boat. Circulation did not appear to be affected by prevailing wind direction although south and south-easterly winds were most common. This may show the Coriolis effect over-riding wind effects. The November 1997 diagram shows flow from the mouth of the Malewa towards the centre of the lake as heavy rains had greatly increased the river flow. This appears small in whole lake terms but carries river water, sediments and associated nutrients into the lake where they will be further transported once caught by the major circulatory patterns. Before in-lake transport becomes important, inflowing river water must reach the lake, especially after rainfall events. There is a lag due to the time taken for water to reach the rivers from their respective catchments and then flow to the lake. This is shown in Table 4.13 which gives depth-profiled productivity measurements for three dates, and indicates that catchment rains takes several days to fully affect the lake. A period of seasonal rains began on 28/3/97, therefore 21/3/97 gives pre-rain conditions, 30/3/97 gives initial post-rain conditions and 13/4/97 allows for a time-lag in transport of river water with associated materials and nutrients.

Table 4.13 Productivity profiles pre- and post-seasonal rains.

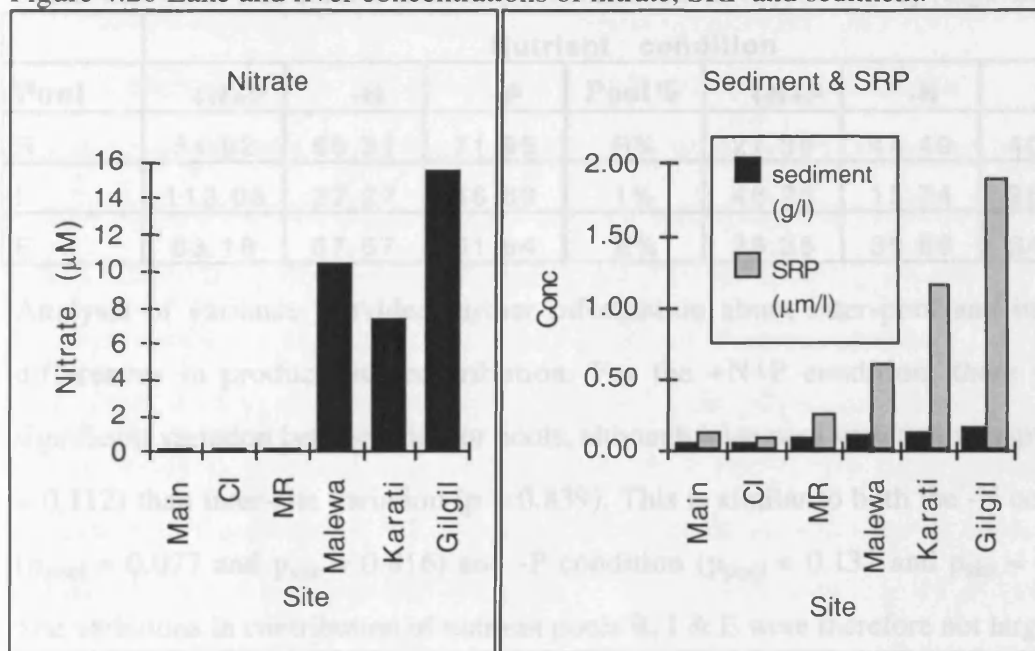
Depth (m)	Productivity (mgC/m ³ /hr) by site and date					
	CI 21/3	Main 21/3	CI 30/3	Main 30/3	CI 13/4	Main 13/4
0	149	147	151	149	145	157
0.25	168	173	179	181	161	-
0.5	204	187	251	209	210	221
0.75	228	214	239	219	240	236
1	227	160	192	118	202	220
2	90	53	82	-	84	61
4	36	21	20	-	27	6

Figure 4.19 Patterns of Main Lake circulation.



The main lake showed a general, though variable, increase in productivity by 13/4/97 but not by 30/3/97 which supports the idea of a time-lag of up to 2 weeks duration (Table 4.13). This only occurred at depths of 1m or less; at greater depths light attenuation over-rides any nutrient effects. The increase did not occur in site CI as it experienced hydrological isolation at that time due to low lake level. Figure 4.20 shows lake and river concentrations for nitrate, SRP and sediments as sampled on 23/4/97. The rivers show much higher loadings than the lake sites including MR, indicating a rapid high dilution factor. There was less river-lake difference for sediment loads although this is still significant ($p < 0.01$) and is correlated with SRP levels ($C_p = 0.956$, $df = 4$, $p < 0.01$).

Figure 4.20 Lake and river concentrations of nitrate, SRP and sediment.



4.3.9 Nutrient pools

Table 4.14 shows the contributions to productivity of recycled (R), internal (I) and external (E) nutrient pools as calculated for Main lake, MR and CI sites in both absolute ($\text{mgC}/\text{m}^3/\text{hr}$) and percentage formats. These results are presented graphically for surface water in Figure 4.22. Site CI productivity profiles are illustrated in Figure 4.23 for each nutrient condition; +N+P (nitrogen & phosphorus added with minor nutrients), -N

(nitrogen omitted) and -P (phosphorus omitted). These show peaks of Internal productivity at 0.5m (approximately the depth of maximum productivity) for +N+P and -P conditions, but for the -N condition there is a peak of Recycled productivity. Surface water of both the main lake and site MR showed reduced Internal productivity under -N (and slightly under -P) conditions and increased Internal productivity under +N+P conditions. There was however little difference between the contributions of nutrient pools in CI surface water under the three experimental conditions. It also appears that changes in the contributions of the 3 nutrient pools to productivity occurred through variations in Internal productivity as the Recycled and External contributions were approximately equal, though variable, at all sites and under all conditions.

Table 4.14 Main lake surface nutrient pool contributions to productivity (mgC/m³/hr).

Pool	Nutrient condition						
	+N+P	-N	-P	Pool %	+N+P	-N	-P
R	64.92	65.31	71.95	R%	27.38	44.40	40.09
I	113.08	22.27	46.69	I%	46.26	15.74	25.24
E	63.16	57.57	61.94	E%	26.35	39.86	34.67

Analysis of variance provides further information about inter-pool and inter-site differences in productivity contribution. For the +N+P condition, there was no significant variation between sites or pools, although inter-pool variation was greater ($p = 0.112$) than inter-site variation ($p = 0.839$). This is similar to both the -N condition ($p_{\text{pool}} = 0.077$ and $p_{\text{site}} = 0.816$) and -P condition ($p_{\text{pool}} = 0.132$ and $p_{\text{site}} = 0.764$). The variations in contribution of nutrient pools R, I & E were therefore not largely due to spatial heterogeneity within the lake despite differences in nutrient regime, hydrological conditions and sometimes overall productivity levels. Inter-pool differences are further highlighted by considering each combination of 2 pools using the Mann-Whitney U-test. Significant differences were seen between pool contributions to productivity for all combinations, sites and conditions except between pools R & E in the main lake for the fully-enriched +N+P condition. There were also no significant inter-site differences. Inter-condition variation (for both absolute and % contributions) was investigated using 2-tailed paired-sample t-tests at $p \leq 0.05$ for significance. There

was a significant difference between +N+P and -N conditions for all cases except pool R. This did not show a difference between any two conditions. R% did show a significant difference between conditions +N+P and both -N and -P, but not between -N and -P as both conditions experience opposite nutrient limiting effects. All other cases showed significant differences except I% between -N and -P, and pool E between +N+P and -P. Correlations of inter-condition productivity contributions (df = 16) were however non-significant in all but 4 cases;

For I%, +N+P & -P gives $C_p = 0.507$ with $p < 0.05$.

For E%, +N+P & -P gives $C_p = 0.614$ with $p < 0.01$.

For I, +N+P & -P gives $C_p = 0.522$ with $p < 0.05$.

For E, +N+P & -P gives $C_p = 0.762$ with $p < 0.001$.

This shows a significant relationship only between conditions +N+P and -P for pools I and E. Condition -N may be uncorrelated as N-limitation was greater than P-limitation in Lake Naivasha and thus caused greater productivity reduction, outweighing other factors. Table 4.15 compares productivity contributions between conditions and shows that productivity contributions of pools I and E were most significantly different between conditions although conditions +N+P and -P were correlated. Comparison with Table 4.14 shows that generally, for pool I, the +N+P condition gave higher contributions to productivity, whilst for pool E it provided a significantly lower contribution. Conditions -N & -P were least different as both showed considerable nutrient limitation although E% still gives $p < 0.001$ with condition -N providing the larger contribution. When considering inter-pool correlations (df = 16), most pairs were significantly, and mostly negatively, correlated as an increase in the contribution of one pool must necessarily reduce that of another. These results are detailed in Table 4.16 (italics indicate non-significance), although some points can be extracted. Firstly, R & E are positively correlated, others negatively; therefore as productivity due to Recycled nutrients rises or falls, so does that due to External nutrients. Secondly, R & I are most closely correlated. This appears intuitive as Recycled nutrients pass through cellular

processes and must thus be temporarily part of the Internal pool, a situation linking the pools functionally. Thirdly, correlations are lowest for the -N condition.

Table 4.15 Comparison between enrichment conditions, main lake surface.

Pool	t-test p-values		
	+N+P & -N	+N+P & -P	-N & -P
R%	0.002	0.004	0.36
R	0.963	0.381	0.387
I%	< 0.001	< 0.001	0.091
I	< 0.001	< 0.001	0.021
E%	< 0.001	< 0.001	< 0.001
E	0.005	0.352	0.028

Table 4.16 Inter-pool correlation of productivity contributions.

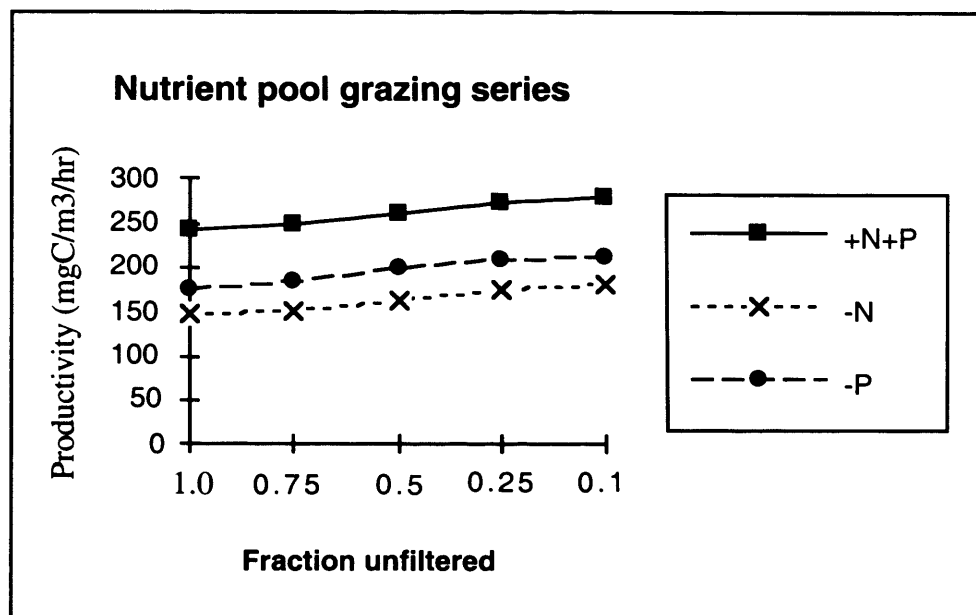
Pools	C _p (probability) by nutrient condition		
	+N+P	-N	-P
R & I	-0.897 (< 0.001)	-0.844 (< 0.001)	-0.855 (< 0.001)
R & E	0.643 (< 0.01)	0.618 (< 0.01)	0.748 (< 0.001)
I & E	-0.501 (< 0.05)	-0.517 (< 0.05)	-0.600 (< 0.01)
R% & I%	-0.991 (< 0.001)	-0.977 (< 0.001)	-0.980 (< 0.001)
R% & E%	0.770 (< 0.001)	0.200 (> 0.1)	0.639 (< 0.01)
I% & E%	-0.848 (< 0.001)	-0.406 (> 0.05)	-0.778 (< 0.001)

Inter-condition variations were also seen for the grazing series obtained in dilution-deletion experiments (Figure 4.21), with productivity values presented in Table 4.17.

Table 4.17 Correlation between dilution and productivity in nutrient pool grazing series.

Fraction filtered	Dilution	Productivity (mgC/m ³ /hr) by condition		
		+N+P	-N	-P
1	0:1	242.81	147.87	174.92
0.75	1:3	249.77	152.25	184.81
0.5	1:1	260.97	163.72	200.16
0.25	3:1	272.14	175.17	209.05
0.1	9:1	278.09	180.04	211.92
r ²		0.944	0.980	0.981
C _p (prob)		-0.997 (< 0.001)	-0.990 (< 0.01)	-0.990 (< 0.01)
% reduction		12.74	17.88	17.16

Figure 4.21 Productivity by nutrient pool grazing series.



For all combinations, ANOVA is $p \approx 0$ when comparing pools therefore each condition produces grazing series with significantly different productivity levels from the others. Correlating the fraction of whole lakewater with productivity for each series thus shows they are very different but closely correlated. Comparing the % reduction in productivity attributable to grazing, condition +N+P is significantly different from both -N ($p \approx 0$) and -P ($p = 0.009$) conditions whilst the latter pair do not show such a difference ($p = 0.664$). This may be interpreted as the +N+P condition inducing greater algal activity and thus reducing the top-down impact of zooplankton. For all pools and all conditions, inter-site variations in productivity contribution were investigated using the Mann-Whitney U-test. No significant differences were found, although valid MR-CI comparisons could not be made due to low numbers of measurements. Similarly, inter-pool comparisons were made for main lake data with results shown in Table 4.18.

Table 4.18 Inter-pool comparison of contributions to productivity, main lake surface.

Pools	Mann-Whitney 'U' p-values		
	+N+P	-N	-P
R vs I	< 0.001	< 0.001	< 0.01
R vs E	> 0.05	= 0.025	< 0.05
I vs E	< 0.001	< 0.001	< 0.01

Figure 4.22 Surface water nutrient pool contributions to productivity.

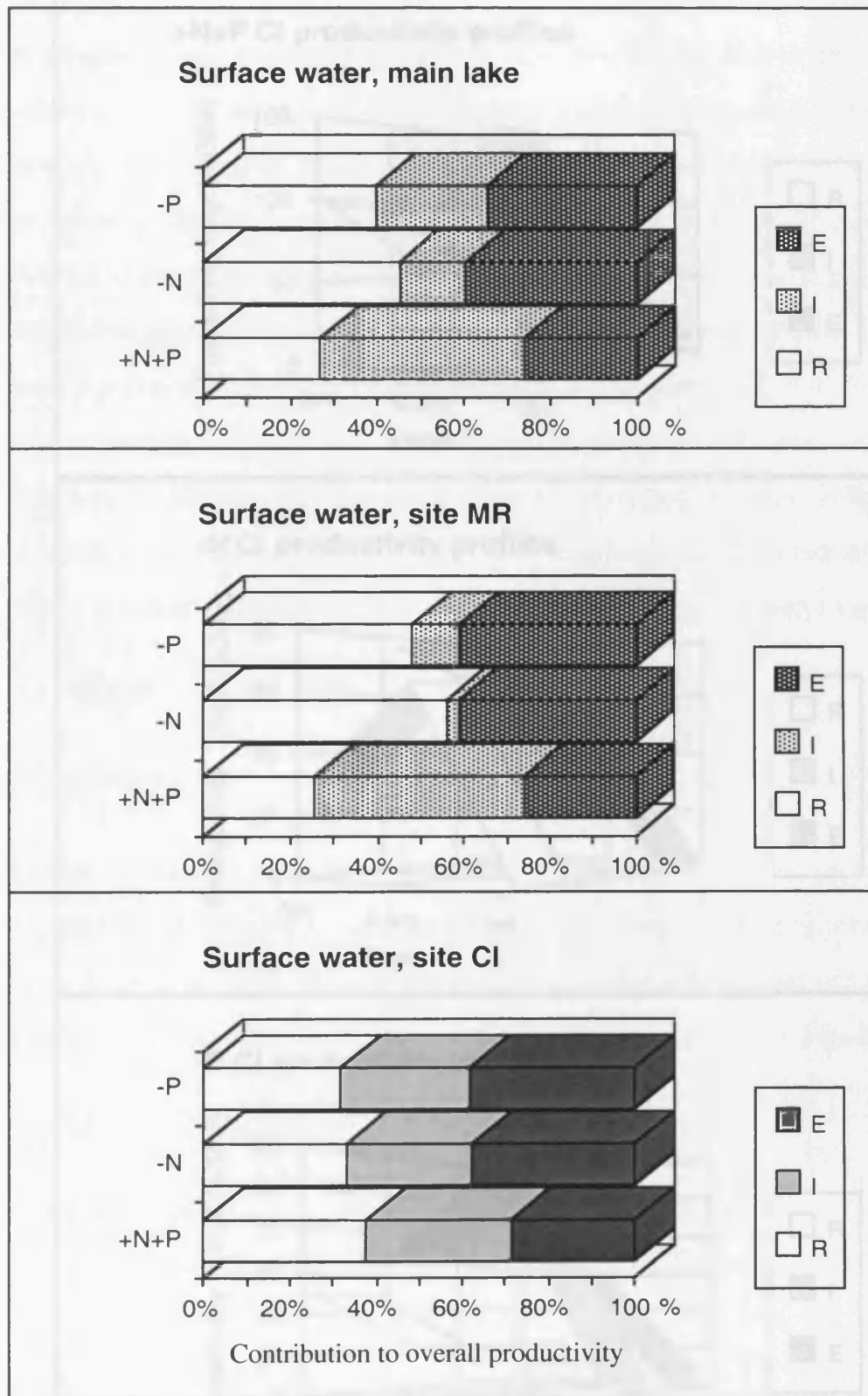
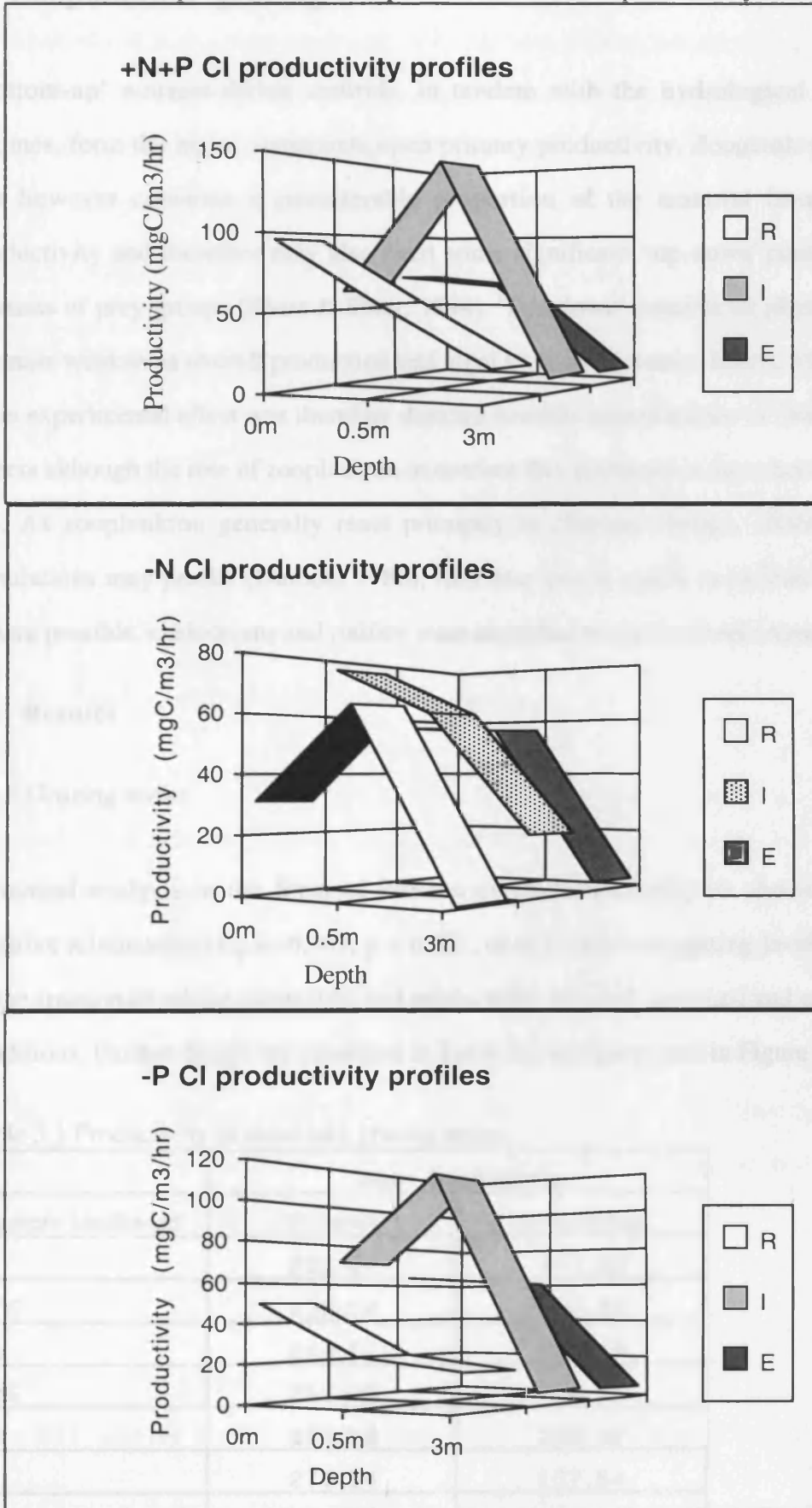


Figure 4.23 Site CI profiles of nutrient pool contributions to productivity.



5. Zooplankton grazing

'Bottom-up' nutrient-driven controls, in tandem with the hydrological and light regimes, form the major constraints upon primary productivity. Zooplankton grazing can however consume a considerable proportion of the material from primary productivity and therefore may also exert some significant 'top-down' control on the biomass of prey groups (Sherr & Sherr, 1994). 'Top-down' controls on phytoplankton biomass weaken as overall production and algal biomass increase (Harris, 1994a). The main experimental effort was therefore directed towards quantification of direct grazing effects although the role of zooplankton in nutrient flux processes is described in section 1.5. As zooplankton generally react promptly to climatic change, although relict populations may persist (Dumont 1980), they may prove useful as indicator species. Where possible, cladocerans and rotifers were identified to species level (Appendix 8).

5.1 Results

5.1.1 Grazing series

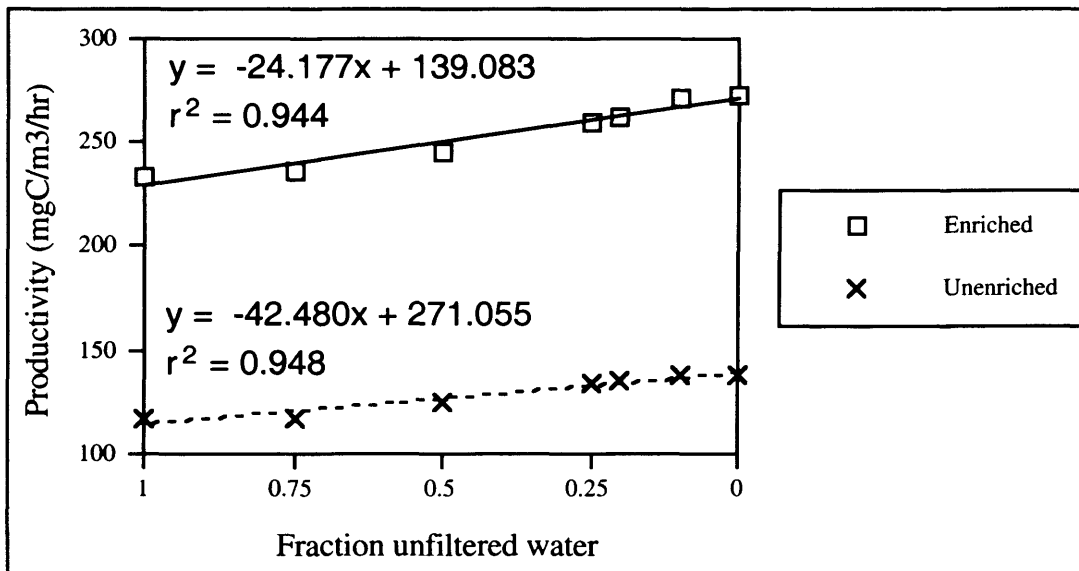
Statistical analysis in the form of Pearson correlation coefficient shows a strong negative relationship ($C_p = -0.987$, $p < 0.001$, $df = 5$) between grazing level (in terms of the fraction of whole lakewater) and productivity for both enriched and unenriched conditions. Further details are presented in Table 5.1 and illustrated in Figure 5.1.

Table 5.1 Productivity in main lake grazing series.

Fraction Unfiltered	Mean Productivity	
	Enriched	Unenriched
1	233.51	117.90
0.75	236.09	117.45
0.5	244.82	125.16
0.25	259.09	134.01
0.2	261.68	135.32
0.1	270.84	137.54
0	272.41	138.50

Comparing via t-test, there is no significant difference between the proportional effects on enriched and unenriched samples ($p = 0.833$) with a mean reduction in productivity of 14.28% (enriched) and 14.87% (unenriched) attributable to zooplankton grazing, as shown in Figure 5.2. Zooplankton grazing can therefore be considered an important, although secondary, top-down control on productivity.

Figure 5.1 Regression of productivity and dilution in grazing series.



Figures 5.1 and 5.2 show grazing effects on productivity values for the main lake and illustrate the difference in absolute productivity values and proportional productivity increase respectively between enriched and unenriched conditions. These linear relationships are the equivalent of the logarithmic equation described in section 2.4.1 (Landry & Hassett 1982). Although the relationships give good linear fits against grazing level for both productivity ($r^2 = 0.944$ enriched & 0.948 unenriched) and proportional change ($r^2 = 0.959$ enriched & 0.944 unenriched), there are also two main non-linear effects involved which can be seen in the productivity data;

1. At low grazing levels, there is no longer any significant top-down control on productivity and a 'plateau' is reached.
2. At high grazing levels, the response is also level until some zooplankton are removed.

Figure 5.2 Regression of proportional increase in productivity and grazing dilution.

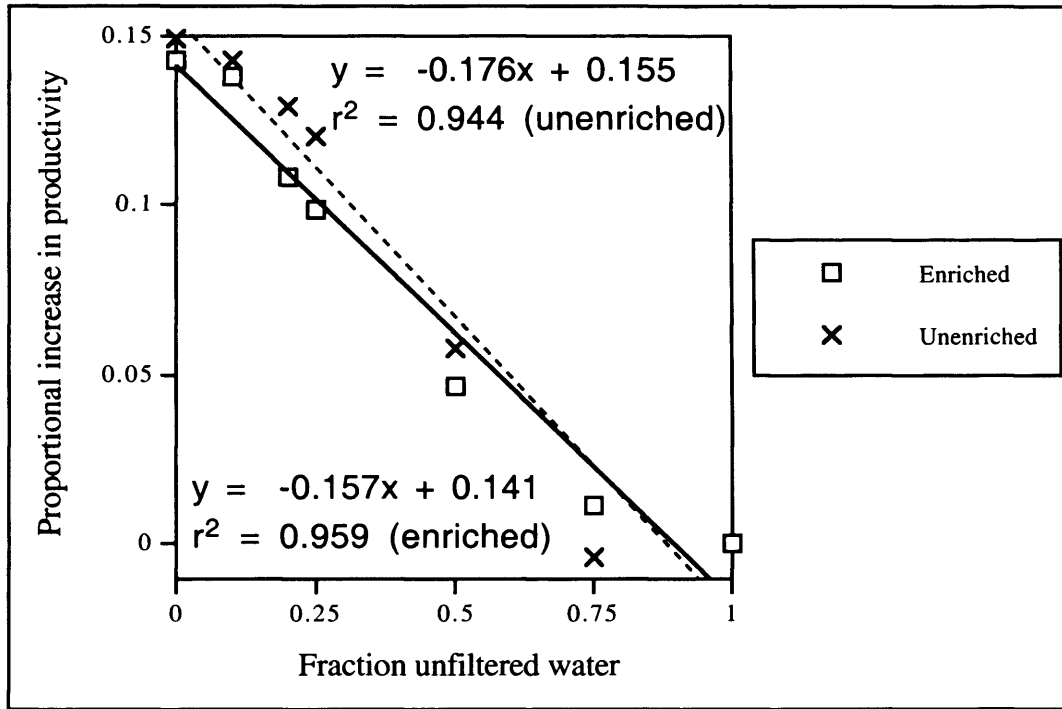
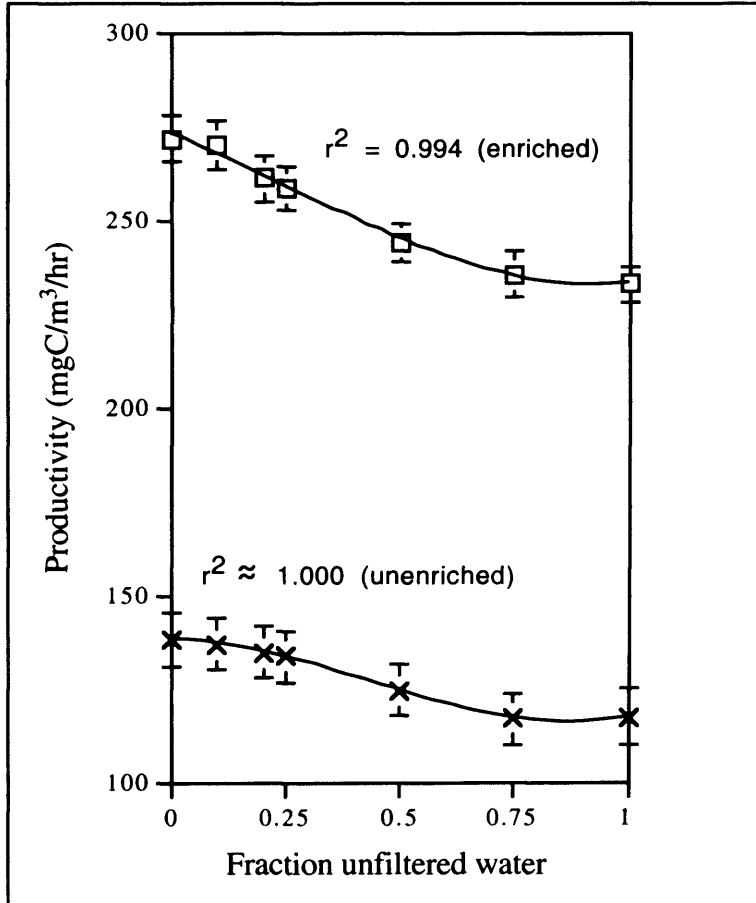


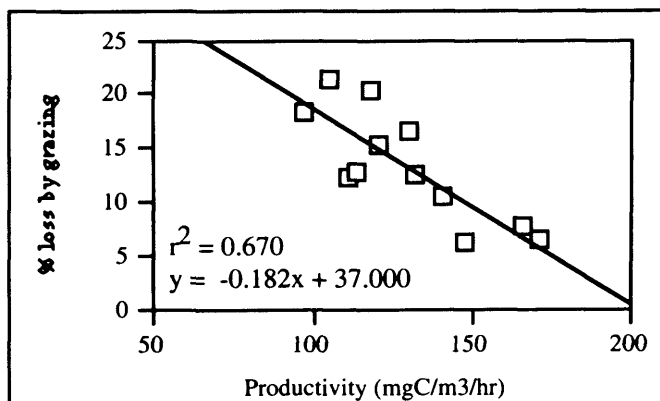
Figure 5.3 Response of productivity to changes in grazing intensity (± 1 S.E.).



For absolute productivity, there is a highly significant difference ($p \approx 0$) between enriched and unenriched conditions, but for proportional change, there is no such difference ($p = 0.185$). Between these high and low grazing states there is a linear response as reduced grazing allows increased algal productivity. These effects produce a more accurate and informative sigmoidal (3rd order polynomial) response as in Figure 5.3 with $r^2 = 0.994$ enriched & approximately 1.000 unenriched. These mean values show good fit with error bars indicating ± 1 standard error (where S.E. = standard deviation $\div \sqrt{n}$). This illustrates the enriched and unenriched series in more detail, showing that although the scatter of data at each point is greater than the range of mean productivity for the series, the standard error clearly separates the two nutrient conditions. This means that although there is a large degree of variation in productivity levels, there is a consistent pattern of response to grazing.

Correlating surface productivity with % productivity loss due to grazing also gives a significant negative relationship ($C_p = -0.807$, $df = 7$, $p < 0.01$). This indicates that the impact of zooplankton grazing as a top-down control becomes less important as productivity increases (Figure 5.4) despite the consistent response indicated by Figures 5.2 and 5.3 above. This indicates that in the lake itself, high productivity will reduce grazing impact, but that this effect requires time to develop, especially as grazers prefer productive cells (section 5.1.2).

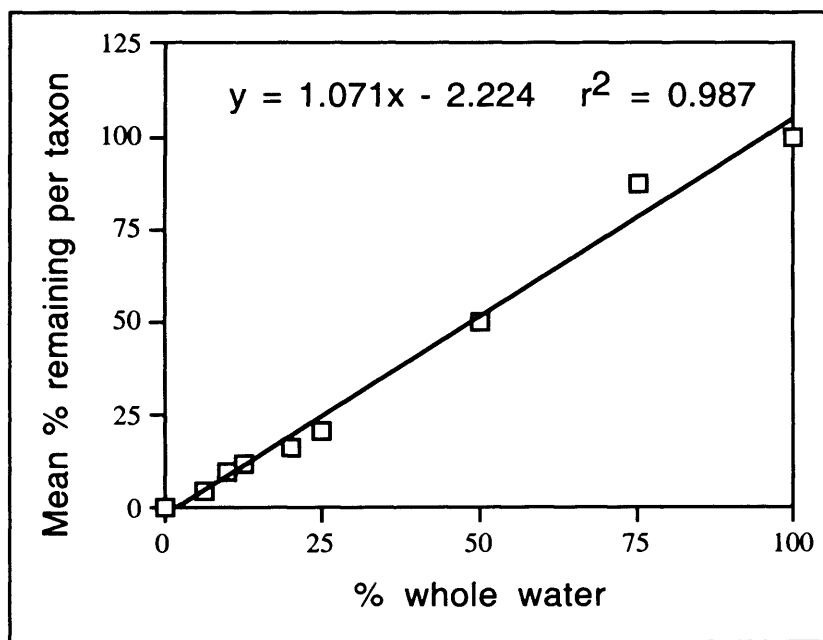
Figure 5.4 Reduction of unenriched grazing impact with increased productivity.



5.1.2 Grazer prey preference

Further analysis was undertaken to investigate grazer preference for different taxa (using *Scenedesmus*, *Aulacoseira*, *Chlorella*, flagellates and cyanobacteria as examples) and size classes (small 'standing-stock' or S-cells and large 'production' or P-cells). Through counting, a planktonic dilution series was developed (Figure 5.5) to confirm that filtering reduced cell numbers by the required proportion and thus that the dilution process itself did not affect results. The r^2 value of 0.987 indicates an accurate reduction in cell numbers with dilution, with a correspondingly high C_p value of 0.994 ($df = 7$, $p < 0.001$).

Figure 5.5 Planktonic dilution series calibration.



When preying on *Scenedesmus*, *Aulacoseira* and *Chlorella*, grazers appeared to prefer P-cells as these were reduced more greatly by grazing activity. Figure 5.6 indicates that P-cells undergo greater reduction by grazing. With lower grazer density there is less prey reduction and P-cells approach the values obtained for S-cells which are grazed at a lower, relatively constant rate. As presented in Table 5.2, these differences are supported by analysis of variance indicating $p < 0.0004$ for differences between S-cell and P-cell grazing reduction for all 3 named taxa. Cyanobacteria are not included here

due to the impracticality of counting cell numbers although a colony size: cell number relationship has been developed for *Microcystis* whilst flagellates are excluded from the statistics by their low counts. A strong grazer preference for P-cells is seen.

Applying ANOVA to investigate differences in %reduction between species shows a grazer preference for *Aulacoseira* as this is reduced more than *Scenedesmus* and *Chlorella*, for both P and S-cells. Similarly, cyanobacteria are grazed less than all other genera, but with no significant difference when compared with flagellates. Flagellates are however grazed less than *Scenedesmus* and *Chlorella*, especially when considering P-cells.

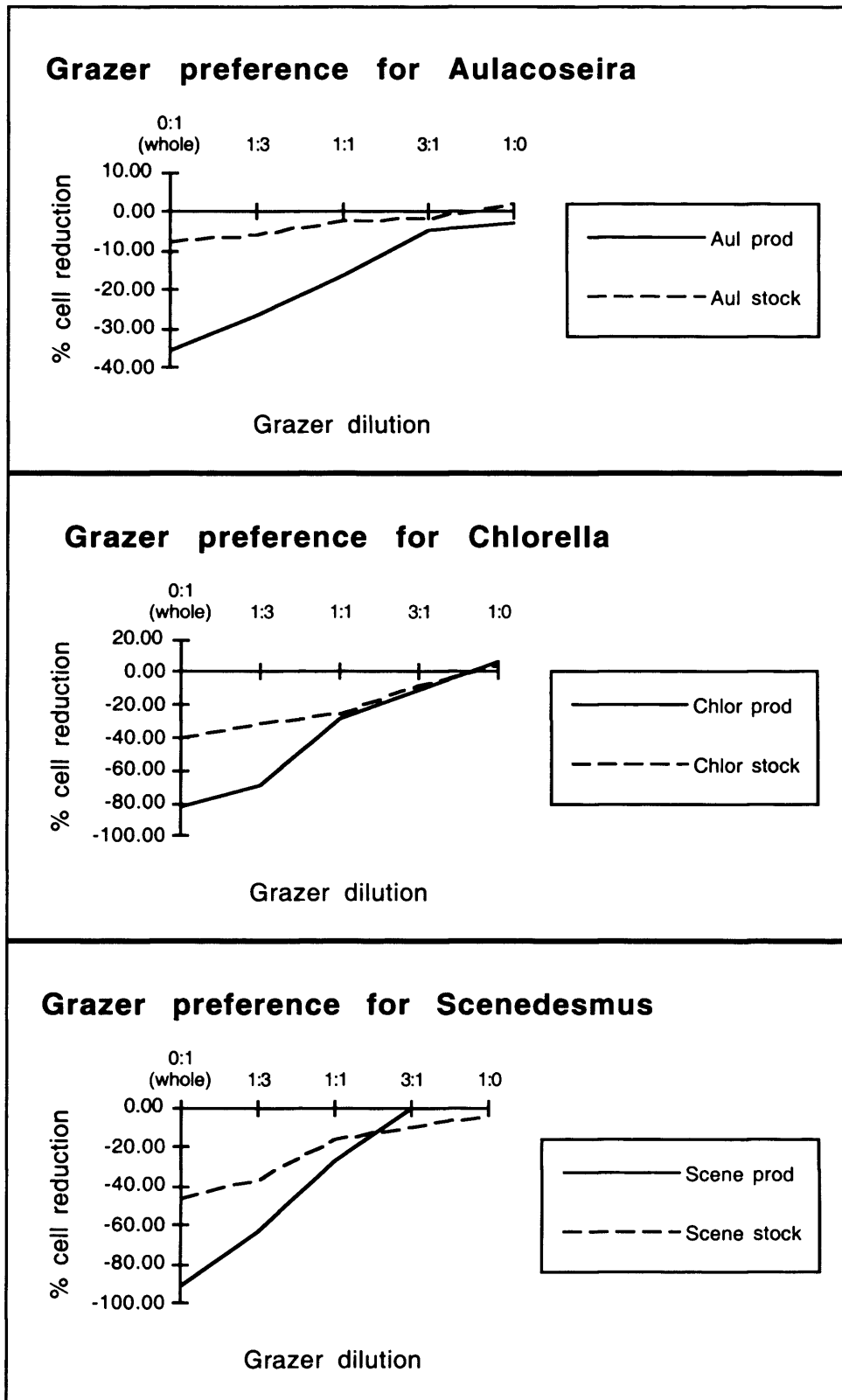
Table 5.2 Comparison of grazing reduction between prey taxa by cell type.

p-values	Stock cells		
Prey genus	<i>Scenedesmus</i>	<i>Aulacoseira</i>	<i>Chlorella</i>
<i>Scenedesmus</i>		≈ 0	0.367
<i>Aulacoseira</i>	≈ 0		≈ 0
<i>Chlorella</i>	0.946	≈ 0	
Production cells			
Prey genus	Cell type	Cyanobacteria	Flagellates
<i>Scenedesmus</i>	Production	≈ 0	≈ 0
	Stock	≈ 0	0.035
<i>Aulacoseira</i>	Production	≈ 0	0.221
	Stock	0.349	0.313
<i>Chlorella</i>	Production	≈ 0	≈ 0
	Stock	≈ 0	0.077
Cyanobacteria			0.442

Given these results, the series of grazer preference starting with the most preferred group is as follows;

1. *Aulacoseira*
2. *Scenedesmus* and *Chlorella*
3. Flagellates
4. Cyanobacteria

Figure 5.6 Changes in prey cell numbers with grazer density showing grazer prey preference for 'production' cells over 'standing-stock' cells.



6. Productivity

Productivity changes may be considered as a disturbance of the balance between photosynthesis and respiration and can give an indication of the sensitivity of a lake system to chemical, or other, impacts. In an aquatic ecosystem all components are interlinked by feedback loops, producing homeostasis, and systems tend to change so as to minimise external stress (Harris 1983).

A number of potential factors may therefore be investigated in order to explain productivity changes as a single perturbation may trigger a chain of events. Conversely, system sensitivity and resilience vary according to which factors are exerting pressure upon the lake and the level of buffering against these pressures. For instance, the effect of eutrophication by algal nutrients depends upon nutrient limitation within the system. Increased productivity may then cause hypolimnetic oxygen consumption and accelerated phosphorus cycling. Phosphate exchange with sediments will be important in shallower lakes, but enhanced by anoxic conditions in deeper water. Anoxic conditions also occur frequently but temporarily in shallow water.

6.1 Results

6.1.1 Levels of Productivity

Levels of productivity at Lake Naivasha are considered as means and variations, both spatial and temporal. Spatial variations can therefore be both horizontal (between sites) and vertical (within the water column as a profile). For instance, Figure 6.1 illustrates productivity profiles and mean productivity levels (23/1/98 to 13/5/98) for surface and 3m water samples, indicating that the deeper sample is more inhibited by high surface illumination, but less restricted by light attenuation (see Section 6.1.4). Table 6.1 shows the profiles of mean Main lake, Site CI and Site MR productivity (23/1/98 to

13/5/98) where lake water was incubated at its sampled depth to measure the natural level of productivity *in situ* without investigation of light-dark adaptation.

Figure 6.1 Mean main lake productivity (23/1/98 to 13/5/98) showing differences in productivity in bottles taken from two different sampling depths.

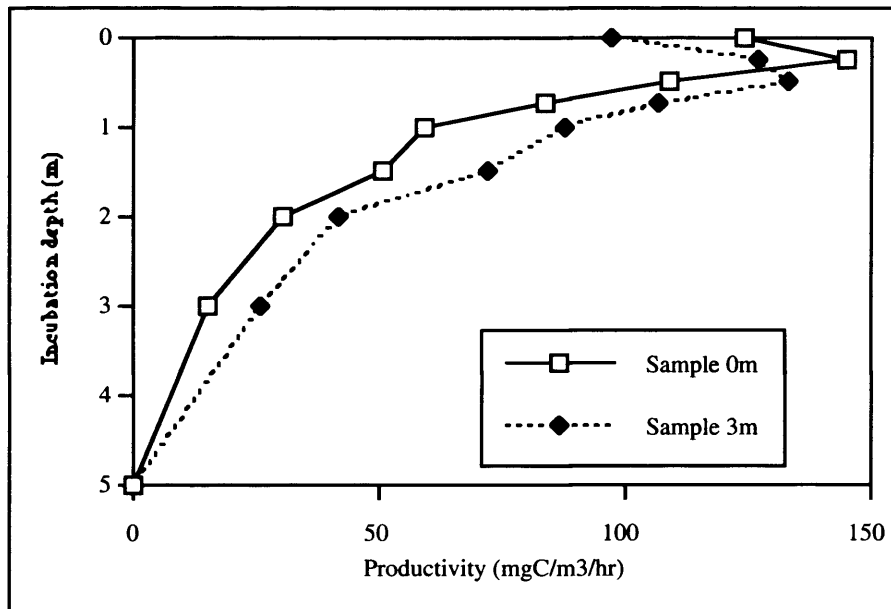


Table 6.1 Lake Naivasha productivity profiles 23/1/98 to 13/5/98.

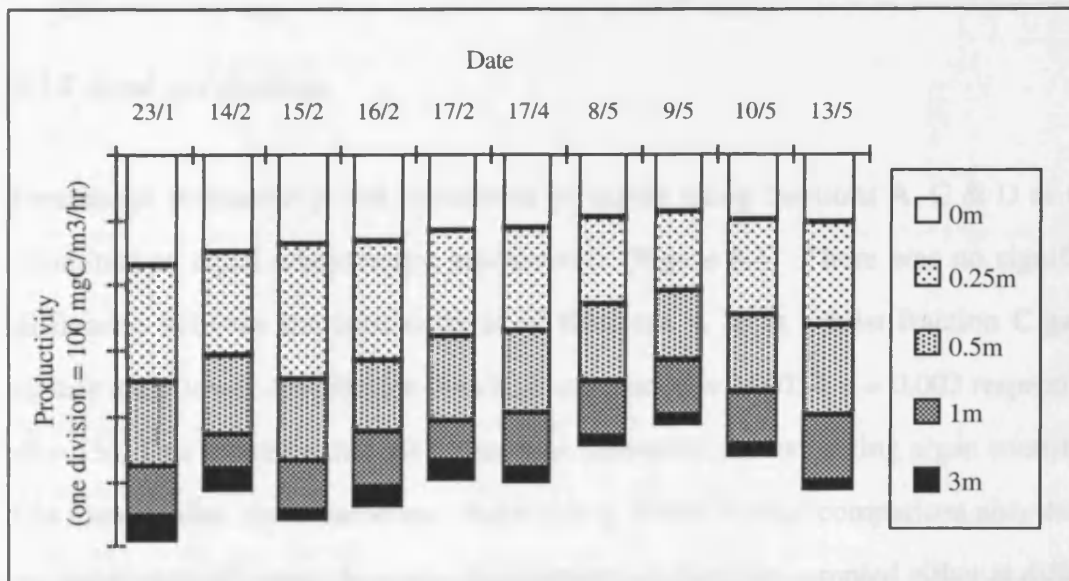
Depth (m)	Productivity by Site (mgC/m ³ /hr)		
	Main	CI	MR
0	124.39	120.35	132.27
0.25	159.58	150.95	154.09
0.5	118.91	145.04	125.49
0.75	97.07	110.6	114.41
1	75.38	80.71	77.12
1.5	62.01		
2	38.73	48.44	38.46
3	25.9	14.5	13.59
5	0	0	

There were no significant differences in productivity between sites, except at 0.5m where Site CI was more productive than the other sites ($p < 0.01$). This indicates that the optimal depth was lower at Site CI due to its greater transparency. Figure 6.2 gives

a time series of Main lake productivity profiles showing changes over time periods from one day to 14 weeks. This shows that daily variations can be as large as monthly changes. In the Main lake, productivity was lowest around 9/5/98 with a peak around 23/1/98. This peak was part of a high productivity period from late January to mid-February 1998. The peak was associated with increased inflow of nutrients from the catchment following heavy rains (possibly related to the El Niño phenomenon) which began in November 1997, and was marked by high *Aulacoseira* numbers.

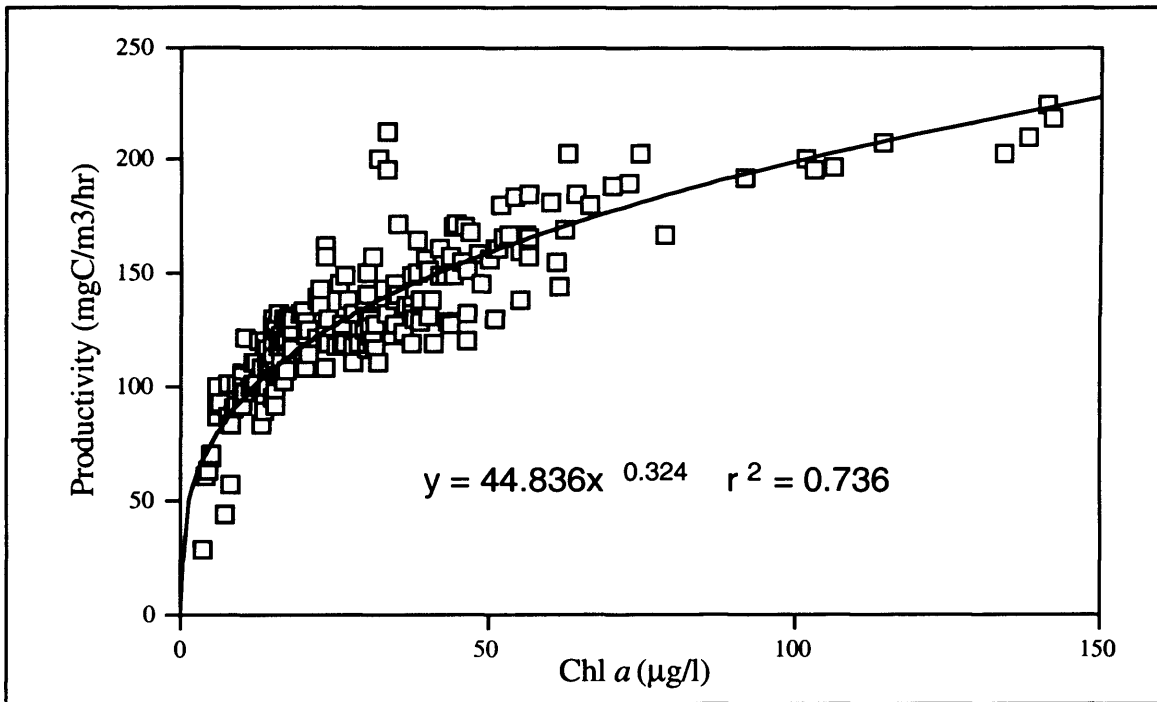
The low-*Aulacoseira* period in May 1998 is also clearly illustrated as a period of reduced productivity. *Aulacoseira* cell numbers and percentage of community were highly correlated ($C_p = 0.766$, $df = 35$, $p < 0.001$) indicating that increases in overall algal numbers and productivity were primarily due to increases in *Aulacoseira*. Cell numbers were highly correlated with maximum productivity ($C_p = 0.863=2$, $df = 7$, $p < 0.01$) but not with surface or suboptimal productivity. This indicates the importance of *Aulacoseira* as a contributor to overall productivity, but that light intensity effects are dominant controlling factors.

Figure 6.2 Main lake productivity profiles 23/1/98 to 13/5/98.



Chlorophyll *a* was strongly correlated with surface productivity ($C_p = 0.823$, $df = 217$, $p < 0.001$) as illustrated in Figure 6.3. Chlorophyll *a* was poorly correlated with phaeopigment measurements ($p > 0.1$, $df = 13$) indicating that phaeopigments and chlorophyll are produced through separate processes and that phaeopigment levels are not linked predictively to primary production.

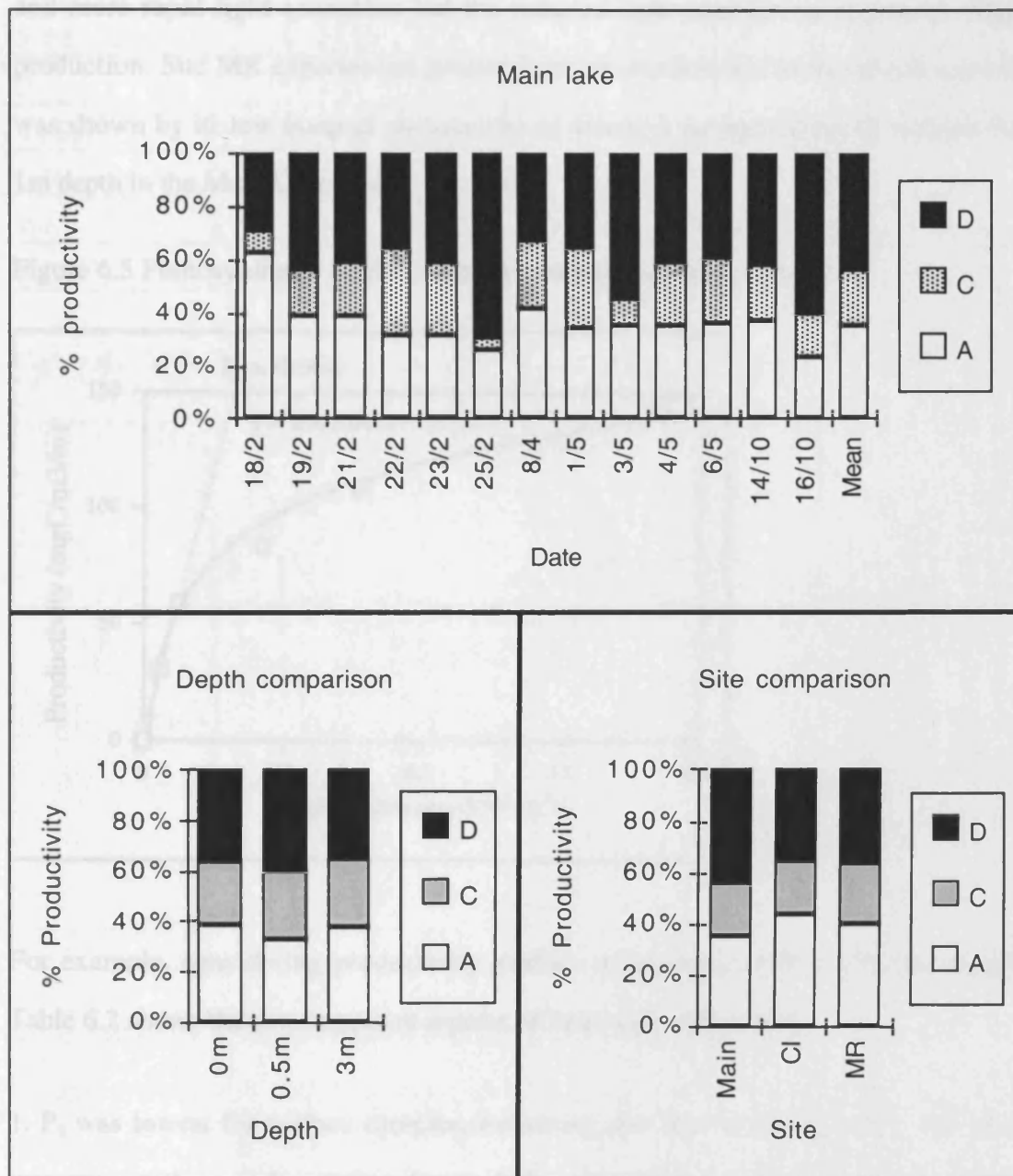
Figure 6.3 Chlorophyll *a*: Surface productivity calibration.



6.1.2 Algal size fractions

Percentage productivity was considered primarily using fractions A, C & D as these combined to equal whole-water productivity (Figure 6.4). There was no significant difference between the contributions of fractions A & D, whilst fraction C gave a significantly lower contribution than both of these ($p = 0.001$ & $p = 0.002$ respectively, $df = 13$). This indicates that the larger, less numerous, slower-acting algae contributed less than smaller, more numerous, faster-acting forms. Spatial comparison also showed no significant difference between contributions of fractions sampled either at different depths (even above and below an oxycline) or different sites.

Figure 6.4 Productivity contributions of algal size fractions.

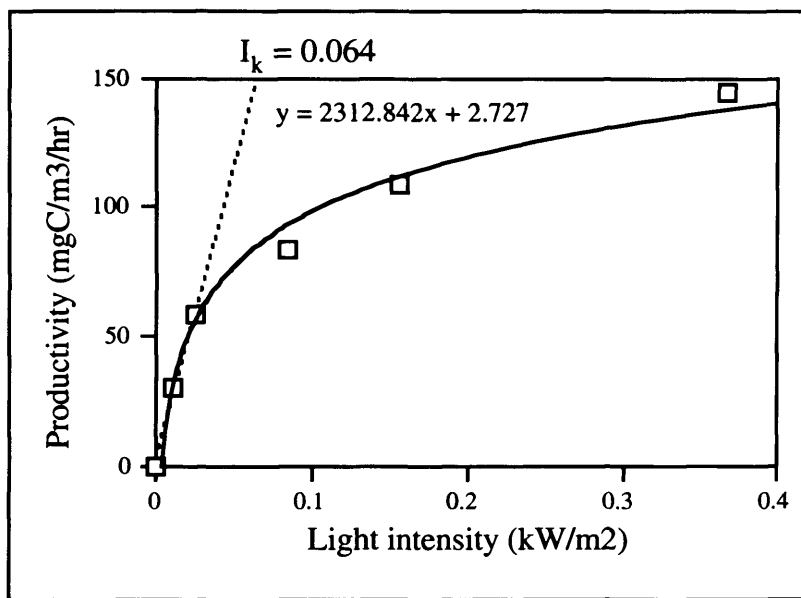


6.1.3 Chlorophyll and photosynthetic efficiency

In the Main Lake (Figure 6.5), $P_s = 1654.44 \text{ mgO}_2/\text{m}^2$, and $f = 19.24\%$, approximately equal to the deeper, clearer water of Lake Windermere on a warm, sunny day. The tropical system may therefore be more productive per unit volume ($P_{\text{opt}} = 159.58$), but is active in a shorter water column. In comparison, for Site CI, $P_s = 2295.27 \text{ mgO}_2/\text{m}^2$, and $f = 17.35\%$, whilst for site MR, $P_s = 1125.52 \text{ mgO}_2/\text{m}^2$, and $f = 18.98\%$. Due to

its greater transparency, Site CI therefore experienced photoinhibition to a greater depth and more rapid light saturation but the reduced light attenuation increased integral production. Site MR experienced greater light attenuation due to its turbidity and this was shown by its low integral photosynthesis which is the equivalent of samples from 1m depth in the Main Lake area.

Figure 6.5 Photosynthesis - light curve for main lake measurements.



For example, considering productivity profiles using samples from different depths, Table 6.2 shows the two important aspects of light-dark adaptation;

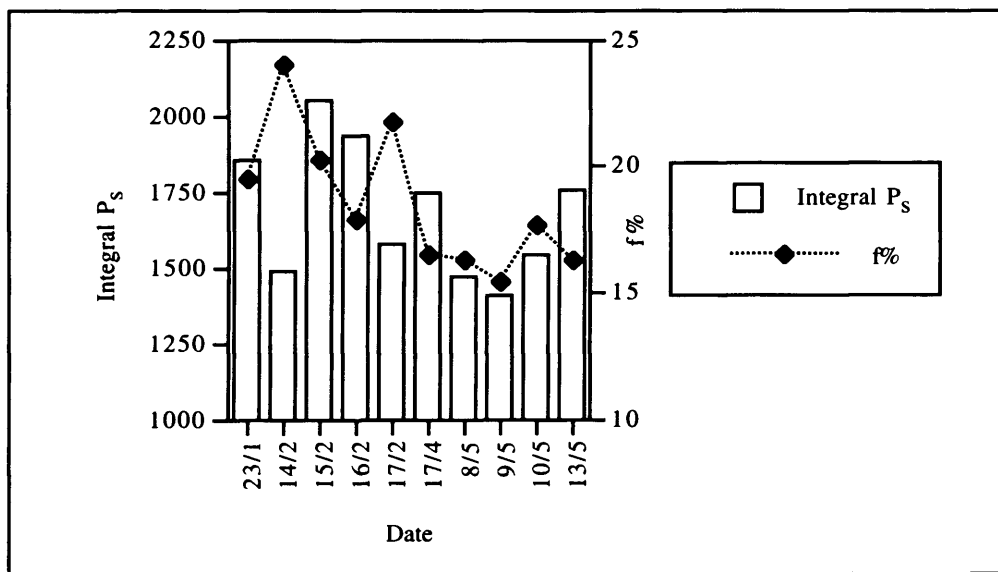
1. P_s was lowest for surface samples, indicating that loss of productivity with depth was greater than surface gains due to light adaptation. Light adaptation (f-values) decreased with sampling depth, indicating that the productivity of dark-adapted samples was more greatly restricted by photoinhibition. Lower light intensities saturated the photosynthetic capacity of dark-adapted algae as confirmed by the reduction in I_k with sampling depth.

2. P_{opt} was greatest between 0.25m and 0.5m where the balance between photoinhibition and light attenuation is optimal.

Table 6.2 Photosynthetic integrals and efficiency with sampling at different depths.

Sample depth	Integral P_s	P_{opt}	f %	I_k
0m	1404.84	144.80	22.00	0.064
0.25m	1557.10	159.58	21.78	0.063
0.5m	1523.57	151.61	20.53	0.058
1m	1496.29	140.57	18.15	0.049
3m	1511.54	133.05	15.65	0.040

Figure 6.6 Main lake Integral photosynthesis and efficiency 23/1/98 - 13/5/98.



Daily variations in integral photosynthesis and efficiency could be as large as monthly changes with high productivity sometimes due to short-term wind-driven accumulation of productive cells (Figure 6.6). There was no significant difference in the % productivity loss due to photoinhibition between Site CI and the Main lake (Table 6.3), but Site MR exhibited a smaller loss than the other two sites ($p < 0.001$) due to greater turbidity. Greater light attenuation therefore reduced site MR productivity below that of the Main lake, whilst site CI was less turbid and more productive. There was also no correlation between f-value and integral photosynthesis ($C_p = 0.078$), indicating that light attenuation is an over-riding factor controlling productivity.

Table 6.3 Productivity and efficiency measurements.

Mean value	Main	CI	MR
% loss by photoinhibition	22.05	20.27	14.16
f%	19.24	17.35	18.98
P_{opt}	159.58	150.95	154.09
P_s	1654.44	2295.27	1125.52

6.1.4 Photoinhibition and adaptation

Productivity profiles (Figure 6.7) followed a standard pattern due to the processes of photoinhibition and light attenuation causing phytoplankton at different depths to be adapted to different light regimes. Deeper samples were therefore more greatly affected by surface photoinhibition whilst surface samples were more greatly affected by reduced light levels (Figure 6.7). These productivity profiles indicate depths where the two effects cancelled and productivity was equal between samples. This 'crossover depth' (D_x) was estimated between samples (Table 6.4). A gradation was found whereby there was an increase in D_x with sample depth for surface incubations due to the differences in light-dark adaptation. Shallower samples were equally productive at shallower depths with a peak (following the general productivity profile shape) at 0.6m for 0.25m samples.

Figure 6.7 Main Lake productivity profiles showing light-dark adaptation.

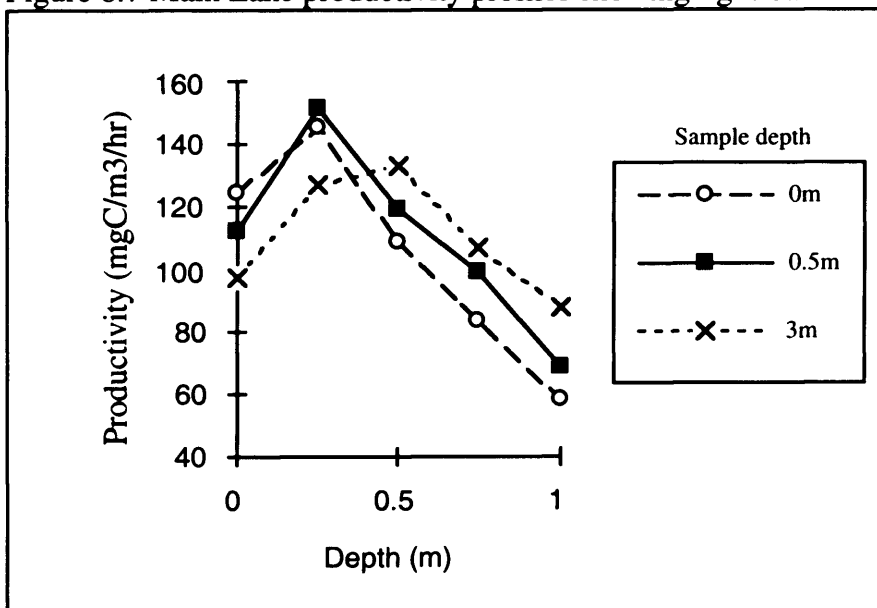
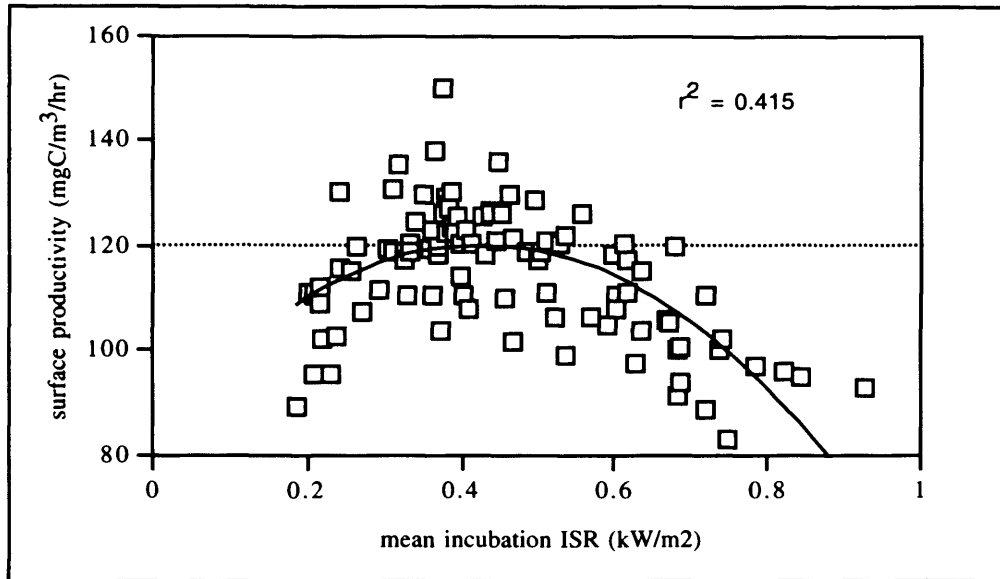


Table 6.4 Main Lake crossover depths for light-dark adaptation.

Sample (m)	Incubation (m)			
	0	0.25	0.5	1
0				
0.25	0.1			
0.5	0.15	0.6		
1	0.3	0.6	0.4	
3	0.35	0.45	0.4	0.4

Comparison was made between surface productivity and mean ISR throughout incubation (Figure 6.8). At low ISR (below 0.3 kW/m²), light was limiting and productivity was below the mean surface value. Between 0.3 and 0.5 kW/m², surface productivity was maximal and relatively level. It was approximately equal to mean productivity as most measurements were made in this range of ISR values. Some measurements used to calculate mean productivity were not included in Figure 6.8 because there was no relevant ISR data. Above 0.5 kW/m², surface productivity was reduced by photoinhibition. Correlating mean ISR with peak productivity suggested a similar pattern but with a weak relationship ($r^2 = 0.217$). Correlating mean ISR with the depth of peak productivity gave a strong relationship ($C_p = 0.754$, $p < 0.001$). As insolation increased, peak productivity was found at greater depth due to increased surface photoinhibition. Maximum productivity was not closely related to the depth at which the peak occurs ($r^2 = 0.046$) although surface and peak productivity were strongly correlated ($C_p = 0.771$, $p < 0.001$). As mean ISR is poorly correlated with peak productivity ($C_p = -0.214$, $p > 0.1$), ISR does not directly determine the level of maximum productivity as it is light-saturated at this point. It did however determine its depth, the extent of photoinhibition and effect of attenuation. The combination of these factors means that ISR affects integral photosynthesis which is important in whole-lake terms rather than only being relevant at a particular depth. This supports results showing that integral photosynthesis rises with light adaptation (Figure 6.6). The resulting increase in productivity at depth therefore outweighs the loss through increased surface photoinhibition.

Figure 6.8 Response of surface productivity to changes in mean ISR. The dotted line indicates mean productivity



6.1.5 Self-shading

Self-shading effects showed a near-linear decrease of productivity with dilution, but an accelerating increase in productivity:chlorophyll (P:C) ratio over the same range (Figure 6.9). The mean ratio rose to a value of approximately 10 whereas individual experiments provided values up to 15 or 20 with plateaux implying a maximum level of 'efficiency' without shading and/or nutrient constraints as separate experiments were run with dilutions made using deionised water and filtered lake water. This implies that the variation between experiments is such that combining experiments as overall mean values obscures some important information regarding these plateaux. Results are therefore separated for 'high' and 'low' surface productivity conditions (above and below 120 mgC/m³/hr, approximately the mean value for these experiments) as illustrated in Figure 6.10 for the Main lake. This shows that for high productivity conditions there is a power relationship between P:C efficiency and reduced shading, whilst for low productivity conditions, this relationship is sigmoidal (3rd order polynomial). As dilution increased, the high productivity condition increased P:C values more rapidly as chlorophyll units approached maximum efficiency. The two conditions met at approximately P:C = 10.39 (10% whole water), very close to the overall mean

maximum value of 10.25. The difference in response form was due to high productivity (i.e. high chlorophyll) conditions being more shaded and thus requiring more dilution to approach maximum efficiency from a lower base efficiency.

Figure 6.9 Self-shading effects on productivity and chlorophyll efficiency.

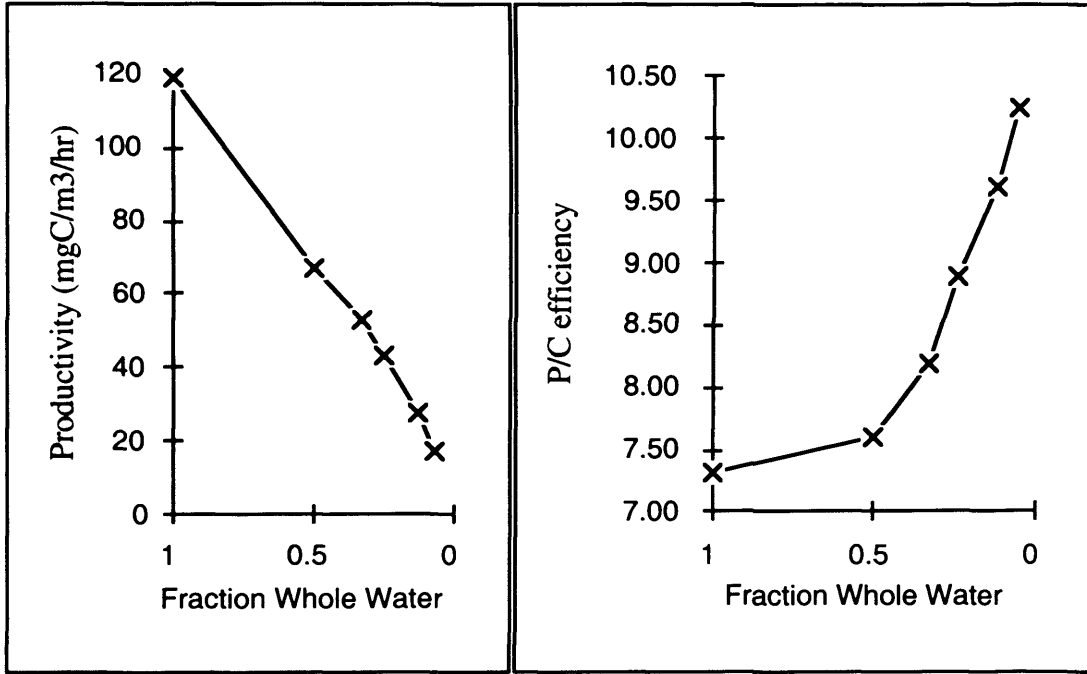
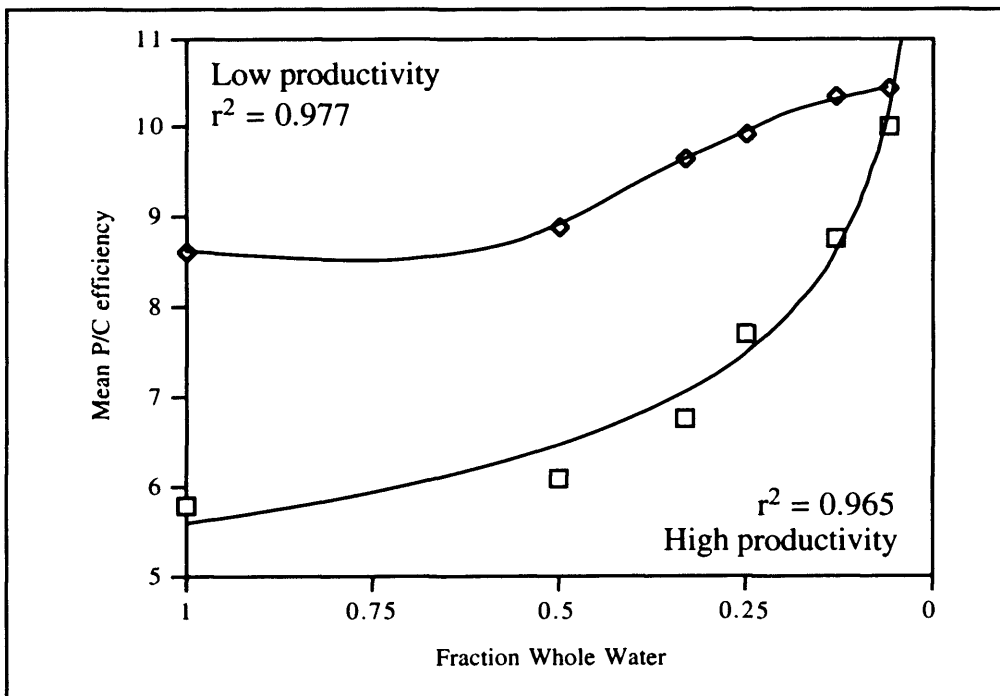


Figure 6.10 Self-shading effects for low and high productivity conditions.



Dividing the overall mean minimum P:C value (7.31) by the maximum value (10.25) gave a figure of 0.71, indicating that 29% of potential production was lost due to self-shading. For low productivity conditions the reduction was 17%, whilst for high productivity conditions it was 46%. Self-shading is thus seen to have had a considerable impact on potential productivity and, especially in conditions of high cell density, may have contributed to the greater rate of light attenuation in the surface metre of the water column.

7. Discussion

7.1 The plankton community

According to Melack (1979b), phytoplankton seasonality in tropical lakes can be split into three broad categories. The most common pattern is that of pronounced seasonal fluctuations corresponding with differences due to rains, rivers or mixing as seen in Lake Oloidien and sometimes Crescent Island lagoon. Developing this idea, a second pattern consists of 'muted seasonality' due to the presence of buffer fringes, perennial rivers and sufficient internal recycling of nutrients. Diel variations are thus greater than longer-term changes and this pattern is seen in Lakes George and Naivasha itself. This means that as the same phytoplankton assemblages can persist for many days, species must be adapted to the full range of environmental variation.

Around its persistent assemblages, Lake Naivasha can however show wide short-term community variations. These occur despite rapid physical and chemical turnover, and the idea that brevity of the mixing period may restrict species fluctuations (Ganf & Horne, 1975). The dominant or 'central' form of the assemblage however remains stable, supporting this idea. This form of seasonality is contrary to the first pattern where there is seasonal succession as species composition changes as conditions change, with species better adapted to the new conditions becoming dominant. A final pattern is that of 'multiple stable points' in the form of persistent assemblages with occasional abrupt shifts between them.

If the benthic 'biofilm' becomes active as light penetration is increased through reduced turbidity and/or lower lake level, chemical processes in the lake bed sediments may be affected. If photosynthetically active, algal biofilms can therefore influence the composition of the solutions overlying the sediment. As photosynthesis removes CO₂ from the water, pH and hence carbonate concentration increase. This leads to precipitation of calcite and coprecipitation of phosphates (Hartley *et al* 1995), a process

which increases with the rate of photosynthesis. For instance, coprecipitation of phosphates reduces the proportion of algally available phosphorus. This may reduce the amount of phosphorus released from sediments, although only during the day when biofilms are photosynthesising.

In a diffuse boundary layer as found in the central part of Lake Naivasha, turbulence of overlying water is suppressed and molecular diffusion becomes the main method of mass transport (Boudreau & Guinasso 1982). Biofilm processes work contrary to this by replacing the process of diffusion from sediment porewater, and are thus able to control chemical fluxes of calcium, alkalinity and phosphorus from the sediment to overlying water (Woodruff *et al* 1999). These processes are not currently important in Lake Naivasha as light attenuation renders biofilms relatively inactive. If this situation changed however, biofilm activity could become one of the processes which immobilise phosphorus in the sediments.

7.1.1 The importance of cyanobacteria in Lake Naivasha

Eutrophication may result in cyanobacterial dominance, with mass developments (blooms) being formed where conditions are favourable. Bloom formation is regulated by light intensity, buoyancy regulation, growth rate, nutrient levels, population stability and temperature (Chorus & Bartram 1999). Blooms may persist almost permanently in some tropical lakes, therefore it is important to understand their functioning in lakes where this is not the case. If cyanobacteria exist in such lakes, what changes in the nutrient budget, or other conditions, are required before they can form regular blooms?

A number of differences in environmental requirements or optima are seen between cyanobacteria and eukaryotic algae;

1. Most cyanobacteria show maximum growth rates at temperatures above 25 °C (Robarts & Zohary 1987), whereas in Lake Naivasha water temperature is usually 20 -

24 °C. With chlorophytes and diatoms exhibiting lower optimal temperatures, the growth rate of cyanobacteria is generally lower than that of algae in the same assemblage (Reynolds 1984). At 20 °C and light saturation (conditions approximating those found in Naivasha), most common planktonic cyanobacteria show 0.3 - 1.4 doublings per day, whilst diatoms achieve 0.8 - 1.9 doublings and chlorophytes reach 1.3 - 2.3 doublings (Van Liere & Walsby 1982).

Due to variation between cyanobacterial species, growth and photosynthesis may be optimal anywhere between 20-30°C. There is also a general preference for neutral pH although the alkaline conditions found in Lake Naivasha are tolerated better than acid. This latter property is due to their ability to utilise low CO₂ concentrations and bicarbonate ions as photosynthetic carbon sources. There is however no simple correlation between alkalinity and species composition, although cyanobacteria have previously been dominant in Lake Naivasha (Kalff & Watson 1986).

2. A low molecular ratio between N & P concentrations may favour cyanobacterial development (Harper 1992b). The optimum N:P ratio for eukaryotic algae is 16-23:1 whilst for cyanobacteria it is 10-16:1 (Schreurs 1992, Chorus & Bartram 1999). Naivasha generally shows ratios below 10:1 which implies conditions are favourable for cyanobacterial blooms. As diatoms remain most dominant, other factors must therefore outweigh the effects of relative nutrient levels.

3. Less zooplankton grazing and the ability to regulate buoyancy contribute to the lower rates of predation and sedimentation loss seen in cyanobacteria than in other phytoplankton. Sedimentation loss is further reduced by regeneration of gas vesicles at depth using carbohydrates allowing colonies to refloat (Utkilen *et al* 1985). These reduced losses help to compensate for their slower growth rate and facilitate greater population stability once established.

4. Where $z_{eu} < z_{mix}$, buoyancy-regulated vertical migration may give a considerable competitive advantage over other phytoplankton by maintenance of a favourable light regime. This is especially true of scum-forming ecostrategists such as *Microcystis*, the most important cyanobacterial genus in Lake Naivasha. In shallow lakes however, this advantage is lost but *Microcystis* can still become dominant, especially in tropical and subtropical regions, and particularly in lakes showing diel stratification (Reynolds 1997). This further suggests that cyanobacterial dominance may increase if stratification becomes more pronounced in Lake Naivasha with possible wind-induced agglomeration as seen for *Ceratium*. If cyanobacteria do become dominant, seasonal differences (unlike in temperate zones) may not be great enough to induce their replacement by algal plankton, allowing domination to be persistent.

In the terrestrial environment, cyanobacteria are often initial colonisers of bare or infertile substrates and the majority are aerobic photoautotrophs (Chorus & Bartram 1999). Despite being primary producers, their most important role may however be as nitrogen fixers (e.g. *Anabaena*), thus contributing to the nitrogen fertility of aquatic habitats, particularly in the tropics. In general, unicellular and filamentous forms are present in most freshwater lakes, especially in eutrophic conditions. In tropical environments, growth may be continuous throughout the year, although they may show a cycle of growth due to physical factors such as mixing. In temperate waters, filamentous forms (e.g. *Anabaena* spp. and *Aphanizomenon flos-aquae*) usually develop first after stratification with unicellular-colonial forms such as *Microcystis* species blooming in mid-summer or autumn (Chorus & Bartram 1999). With Lake Naivasha's "summer" conditions, *Microcystis* species are the most prevalent form of cyanobacteria. The main factors which seem to affect non-blooming cyanobacteria appear to be light, temperature, pH, nutrient concentrations and the presence of organic solutes (Rosén 1991). Most planktonic forms grow best at relatively low light intensities sufficient to saturate their photosynthetic systems with many cyanobacteria unable to survive sustained high light intensities. Cyanobacteria also show a favourable energy balance with little maintenance energy required and can therefore grow at a

higher rate than other phytoplankton at low light intensity (Van Liere *et al* 1979). This confers a competitive advantage in turbid waters or where algal plankton are numerous and shading. At greater intensities, photoinhibition occurs and other species may be prevalent.

Buoyancy regulation is therefore undertaken by species such as *Anabaena flos-aquae* and *Microcystis* spp. using gas vesicles to maintain a favourable light regime (Reynolds *et al* 1987). This means the presence of such species can not be strictly related to the level of eutrophication, although their maximum biomass does depend on eutrophication. Most *Microcystis* blooms are therefore found in lakes with summer Chl *a* concentrations of 20 - 50 µg/l and Secchi transparency of 1 - 2 m (Chorus & Bartram 1999). These conditions would be approximated in Naivasha if transparency increased (e.g. through dilution as seen following the El Niño rains). The last time transparency was in this range, Naivasha was still oligotrophic and thus cyanobacteria were not dominant. Cyanobacteria are somewhat less dependent than algae on fluctuating nutrient supplies as they can store excess nutrients for later use, with heterocystous forms able to use atmospheric nitrogen directly if necessary (Moss 1998).

An increase in organic solutes correlates with increased cyanobacterial populations through the oxidative metabolism of organic substrates. This results in reduced oxygenation, which in turn stimulates both photosynthesis and nitrogen fixation. Many cyanobacteria grow attached to rocks (epilithic), plants (epiphytic) or sediments (epipellic) in lakes, and in shallow lakes such as Naivasha, attached forms may contribute significantly to overall productivity. Benthic forms may be responsible for occasional peaks of nitrogen fixation in oligotrophic lakes (Metz *et al* 1997), with eutrophic epipelon species commonly including genera such as *Aphanothece* and *Nostoc* (Round 1981). The epiphyton however is likely to be dominated by diatoms and chlorophytes. Cyanobacterial abundance may pose problems in areas such as reservoirs, but is very important in situations like the maintenance of soil fertility (Youdeowei *et al* 1986) and thus is worthy of consideration in many aquatic studies.

7.1.2 *The microbial loop and size fractions*

The plankton communities of lakes Naivasha and Oloidien are both numerically dominated by organisms with cells smaller than 5 μm . In Lake Naivasha, this fraction is itself dominated by the picoplankton near the surface, but at a depth of 4m or more, the smaller attoplankton are dominant. This is seen in both the Main lake and Crescent Island lagoon, therefore temporary stratification does not affect the distribution of size fractions. Below the euphotic depth (approximately 3m) there is less than 1% of incident sunlight remaining (Moss 1998) and primary production is much reduced, reaching zero at a depth of 4 - 5m. The attoplankton include the bacteria and become more numerous and dominant in this region presumably through non-photosynthetic production. There is also less dissolved oxygen at depth which favours anaerobic forms, especially at the sediment-water transition zone where conditions become increasingly anoxic. Macek (1992) shows ciliate distribution to be affected by epilimnion position with most at the bottom of the euphotic zone where there is much phytoplankton decay and low DO. This was not seen in Naivasha due to the turbulent water-column. Micro- and nanno-plankton cells are found below the euphotic depth due to mixing, but are unproductive, with some lost to sedimentation despite turbulence. Much of the picoplankton consists of cyanobacteria such as *Microcystis* which show buoyancy regulation (Moss 1998) and can remain nearer the surface. In Lake Oloidien, there is almost complete dominance by such picoplankton throughout the water column. There are also much greater absolute numbers of cells despite high turbidity and self-shading producing rapid light attenuation. This suggests that photosynthesis is inefficient in most cells, and that there is much non-photosynthetic production by bacteria, and possibly other sources such as heterotrophic flagellates. The contribution of heterotrophy to algal growth is however considered to be small (Round 1981). Lake Naivasha contains greater proportions of nanno- and micro-plankton than Oloidien, consisting largely of photoautotrophs such as the dominant *Aulacoseira*. Protozoa and larger zooplankton are however found in very small numbers at all sites despite exerting a secondary control on primary productivity. The presence of few protozoa in a trophic

cascade implies that they are out-competed for small food particles by small cladocerans and there is a jump across one layer in the trophic cascade (Carpenter 1988). This may be because larger cladocerans are predated, especially during the period of post-El Niño fish population recovery as noted by personal observation. This indicates that ‘sloppy feeding’ is a minor source of nutrients, especially in eutrophic conditions. The microbial loop is relatively unimportant as an active community of algivores is required to release carbon (Straskrabova & Simek 1993). It also suggests that grazing impact is primarily due to larger heterotrophs such as cladocerans. This is supported by investigation of grazer prey preference (section 7.3.1) which shows that cladocerans prefer food sources which they can utilise efficiently without handling problems (e.g. *Aulacoseira*).

7.2 Chemical and Physical conditions

Major nutrient input is due largely to riverine transport, with flow and nutrient load regulated by climatic and anthropogenic factors. Both sediment-bound and soluble nutrients are transported into Lake Naivasha by river water. 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. TP levels show little difference between the main lake and site CI, however site MR has higher TP loadings at all depths, especially at 1m and below. This is unsurprising as phosphorus is transported bound to sediment particles with the Malewa as the main source of sediment input due to upstream erosion and the lack of any other major rivers. Sediment is therefore transported into the lake with a noticeable underflow 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 nitrate series correlating less closely with changes in SRP than changes in NH_4 indicates that the increased availability of nitrate due to enrichment outweighs some of the algal preference for ammonium. SRP concentrations indicate that as well as differences in processes above and below the oxycline, there are also processes causing

variations in conditions within mixed layers. For instance at approximately 0.5m - 1m depth there is maximal photosynthesis 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.

7.2.1 Nutrient pools

Data from separation of nutrient pools and their contributions to productivity also provides information about the dynamics of major nutrients. The peaks of Internal productivity seen at site CI at 0.5m depth where productivity is maximal may be due to recycling of nutrients being unable to meet demand and thus intracellular material being used. For the -N condition, the peak of Recycled productivity may be caused by phosphorus enrichment and rapid recycling of phosphorus as SRP (Talling 1993) creating nitrogen limitation. This in turn requires nitrogen to be recycled to maintain levels of productivity. The Recycled pool does not show a difference between conditions as the rate of nutrient recycling by planktonic primary producers is extremely rapid. This means only small quantities of nutrient are required unless a balancing nutrient is in excess causing increased limitation.

Condition -N may be uncorrelated with other conditions as N-limitation is greater in Lake Naivasha and thus causes greater productivity reduction, outweighing other factors. Pools I and E may be important because the Recycled pool provides nutrient requirements and thus is less affected by enrichment. In the fully enriched +N+P condition, pool I shows higher contributions to productivity, whilst for pool E this is lower. This is opposite to the intuitive implication that enrichment should make the external nutrient pool most important, possibly due to nutrients being rapidly taken into cells (e.g. Kalff 1983) and becoming part of the internal pool during incubation. With external nutrients in excess however, condition +N+P does give a higher contribution for pool E than -N as the latter condition is most limiting. This also helps to explain the lower pool R contribution under +N+P conditions as less recycling is required.

7.2.2 Nutrient dynamics

Considering minor nutrients, the higher concentration of sulphates at site MR is attributed to riverine transport. Silicate levels are lower at site CI because silicates are also transported into the lake in river water, and then utilised by diatoms which are often particularly numerous in Crescent Island lagoon. Silicate concentrations also show variation with depth due to differential use by algae as 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 show much difference between sites, remaining low ($<20\mu\text{M}$) from the surface to 2m depth, with a small steady increase below this as there is reduced algal activity and nutrient uptake due to light attenuation. This effect outweighs that of mixing as the rates of nutrient uptake and cycling are greater than those of hydrological turnover. 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.

TN levels are also similar at main lake and CI sites, however the concentration is much higher at site MR. Here there is much inflow of suspended and dissolved material including runoff from livestock which have been watered upstream. This is especially relevant during high rainfall periods when high water levels flush collected material downstream. This inflow of material can be seen by considering the levels of TSS in each of the 3 inflowing rivers over a number of months. Differences over time relate to transitions between high and low rainfall periods. In the River Malewa, increases in TSS, PP, TP and TN occur (largely between 2.5 and 35.5 km downstream) because rains have caused erosion and subsequent transport of sediments and nutrients. Further downstream the river is less erosive and enters a depositional phase, also diluting its contents by having greater volume. The importance of nutrient transport and circulation is enhanced as there is underflow of river water further into the lake than is evident from water nearer the surface, an effect illustrated by transects taken from the Malewa

rivermouth towards the lake centre. As much of the papyrus fringe has been cleared from the northern shore (Harper *et al* 1990), there is reduced buffering and consequently an enhanced gradient of reduced nutrient concentration moving away from the northern inflow points 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 (e.g. *Ceratium* mass at MR). 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, however temperature reduction is sometimes detected without recording deoxygenation. 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.

With nutrient profiles covering SRP, TP, NO₃, NH₄ and TN produced for all sample sites at depths from 0 to 7m, much information can be derived about spatial variation of nutrients. Where a saturated point has been added to a detailed low concentration series, it is important to note that this only provides a maximal productivity level, and that the response curve between high and low concentrations will show aliasing, and subsequently appear to continue rising albeit at a slower rate. The differences between series are seen at both low and saturated concentrations, and also at site CI. 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, at least at a basic level.

7.2.3 The importance of mixing regime

Beginning with phosphorus fractions, SRP shows a lower concentration above 3m at site CI than in the main lake or Malewa Rivermouth site (MR). Below 3m, this situation reverses due to anoxic release of phosphates as this is the only site to undergo regular

stable stratification. This nutrient release does not appear however to affect productivity either locally (as productivity is not significantly higher in CI) or in whole lake terms, especially as any nutrient-rich waters from below 3m in CI would be greatly diluted once transported elsewhere by currents in the lake. Even within Crescent Island lagoon itself (diameter 1.3km, depth 18m) the water below 3m only constitutes approximately 57% of the total lagoon volume (0.008 km³) and thus this relatively nutrient-rich water is diluted by half if the lagoon mixes. Phosphorus resupply from sediments therefore occurs but due to the lack of temporary stratification, is less important than water-column recycling. Although partially separated from the rest of the lake and usually less turbid, CI receives nutrients from water flow and associated suspended sediments, with possible but untested faecal input from the artificial concentration of grazing mammals on Crescent Island itself. When the lake level is low, the separation of Crescent Island lagoon is accentuated until only a single narrow channel remains. This greatly reduces the influence of the main lake upon the lagoon and is most noticeable in terms of reduced turbidity as suspended matter such as sediment settles out without replacement by new inputs. Measurements of DO and water temperature (section 4.1.2) show that increased physical isolation affects the mixing regime of the lagoon, as stratification only occurs at this site. The similarity in conductivity between MR and Main lake indicates early mixing of dissolved solid loads transported by the River Malewa, although MR samples were often taken 'downstream' from the true rivermouth due to impenetrable blockage by *C. papyrus* islands. With the period around 2/10/98 showing conditions closest to temporary stratification in the Main Lake as well as the regular CI stratification, there may be occasional stratification within the Main lake but this is weak and very temporary as afternoons are almost always windy. This suggests that more complete temporary stratification may occur if the lake deepens further, allowing possible nutrient release with greater deoxygenation. Such a change would produce a localised source of nutrients in site CI with short-term nutrient release. Currently, the only large localised productivity increase has been temporary wind-driven accumulation of phytoplankton near site MR. As yet there is no localised increase at site CI although

sediment nutrient release is seen. Such P resupply may augment internal nutrient cycling and external input from rivers. Reduced mixing may allow sedimentation to become an important algal loss factor.

The results (section 4.1.1) indicate that completely calm periods of more than 8 hours are required to significantly impact upon productivity through sedimentation loss. There would also need to be time for ongoing mixing to cease. Sedimentation is potentially important because *Aulacoseira* shows almost total loss of cells without mixing, and is the dominant genus in Lake Naivasha with a major contribution to productivity. With some forms able to regulate their buoyancy, cyanobacteria show much smaller losses, suggesting a change in mixing regime would also change dominance in the algal-bacterial community. Motile flagellates (especially *Mallomonas* which was relatively abundant during sampling) can maintain their position in the water column and show increased cell numbers as production and cell division are able to continue, possibly at a faster rate as algal shading is reduced. *Staurastrum* also shows increased cell numbers, possibly due to buoyancy related to cellular spines, although cellular counts were low and could merely be due to random variation in the data. The smaller reduction in productivity than cell numbers indicates an increase in photosynthetic efficiency with reduced cellular shading. Continuing measurements show there is little further change after 8 hours as such a large proportion of cells are already lost. It is presumed however that in a situation of prolonged water-column stability, algal forms possessing buoyancy regulation would increase as other taxa were sedimented, allowing a shift towards cyanobacterial dominance. The 57.35% reduction in cyanobacterial numbers during this experiment indicates that non buoyancy-regulating forms dominate in Lake Naivasha during mixed conditions. This follows Reynolds (1992) who states that as mixing dominates over buoyancy forces, there is less opportunity for spatial segregation, interaction between species, competitive exclusion and individual behaviour. Mixing determines the vertical light gradient experienced by cells and chemical composition, especially in deeper water. Subsequently, there is less opportunity for a change in dominant species and long-term dominance of *Aulacoseira* is seen. The importance of

light regime has been shown in comparable systems such as Lake Okeechobee, Florida (Phlips *et al* 1995) where light attenuation is primarily related to the concentration of suspended matter, and chlorophyll *a* concentration is positively correlated to light availability in the epilimnion.

7.2.4 *The importance of climate*

Lake level is not generally correlated with local rainfall, but may be related to longer-term large-scale climatic events (Vincent *et al* 1979). Trends in water levels of larger, deeper Tanzanian lakes show a close relationship with catchment rainfall variability, but with a 2 - 5 year lag (e.g. Lake Tanganyika, area 32600 km², catchment 198400 km², mean depth 580 m). Shallow closed basins (e.g. Lake Rukwa, area 3700 km², depth 0 - 3 m) show more rapid responses to increased rainfall, but levels can only fall when evaporation exceeds input (Nicholson 1999). The most direct relationship is between annual catchment rainfall, which falls within the same range as Lake Naivasha, and the change of lake level during the course of the year. There is a relationship between lake level and local rainfall only for high rainfall events and the permanent state of annual evaporation always exceeding annual precipitation (Harper *et al* 1990). Lake level changes in September are related to the total July to September rainfall at altitudes of at least 2500 m. Water level fluctuations have implications for the nutrient status of lake water through effects on macrophytes and agriculture (Harper *et al* 1995);

1. Water level decrease or stability allows crop or livestock farming to follow the lake edge through burning, leading to loss of *Cyperus* buffering. Rising water levels threaten loss of farmland, and there is some recovery of natural vegetation.

2. A decline in level (allowing soil and seed drying), followed by a rapid rise causes reflooding of an uncolonised band, and subsequent *Cyperus* germination. This helps to maintain a buffer strip and in the north of the lake, the shallower slope and greater areal changes allows swamp development. This development is not seen if the reflooded strip has been colonised by grass. *Cyperus* may be submerged and die if the water level rises

although weakly rooted sections may become part of the floating raft. Sections of this raft may reroot in waterlogged soil if stranded during a decline in water level. Such islands are larger and more numerous shortly after a lake level rise.

3. Water level rise also releases dried, oxidised nutrients from reflooded soils, whilst reduced lake level leads to nutrient concentration (Harper *et al* 1993). Nutrient release depends on previous land use as soil nutrient levels will be higher if they have been used for farming with application of fertiliser or deposition of animal waste. Consideration of climate data shows rainfall to be the dominant climatic factor in the determination of seasonality, defining seasons such as 'dry', 'short wet' and 'long wet'. Seasonality is therefore due largely to the bimodal annual rainfall pattern at Lake Naivasha, although during this study the rainfall pattern has been atypical. Drought conditions prevailed in early 1997, with excessive (possibly El Niño-driven) rainfall and flooding from late 1997 until mid-1998 followed by further drought as the November 1998 short rains failed. As there is no long-term trend in rainfall, changes in productivity can not be directly related to climatic effects. Separation of climate data into 'types' also provides no direct link between climatic factors and productivity. Other factors show no clear trends unless linked directly to rainfall, instead varying around a longer-term pattern. Rainfall is therefore the only climatic factor which may control changes in productivity or algal community. Work by Becht (in press) shows that lake levels can be accurately simulated from both the amount of river inflow and catchment rainfall. After 1985 however, observed lake level is lower than simulated levels, an effect attributed to water loss by abstraction.

7.3 Zooplankton grazing

Zooplankton grazing is seen to be an important top-down control in Lake Naivasha, and therefore potentially in other tropical freshwaters. The effect is however secondary to both light effects which dominate the photosynthetic system, and bottom-up nutrient limitation which effectively halves the potential productivity.

As well as a reduction in productivity with grazing there are two other effects involved;

1. At low grazing levels, there is no longer any significant top-down control on productivity and a 'plateau' is reached with those grazers remaining feeding at a maximal saturated rate.
2. At high grazing levels, grazers are feeding sub-maximally due to competition for food and thus grazing pressure is not reduced until enough zooplankton are removed to fall below this level.

Between these states is the linear response as reduced grazing allows increased algal productivity. The impact of zooplankton grazing as a top-down control also becomes less important as productivity increases. This relationship (illustrated in Figure 5.6) implies that, for natural waters, grazing impact should become negligible when productivity reaches approximately 200 mgC/m³/hr. With experimental nutrient enrichment raising productivity above this level, there is still a similar response with significant top-down control. Unless the relationship is actually curvilinear, this suggests that artificial nutrient enrichment may increase algal susceptibility to grazing and/or zooplankton grazing activity, or that the measured level of productivity is higher than the true value. As productivity is closely related to *Aulacoseira* numbers, grazing control is also of reduced importance during high-*Aulacoseira* periods.

7.3.1 Grazer prey preference

The preference of grazers for Production cells may be due to a number of factors;

1. Production cells store nutrient for use in division and growth, and thus should be of greater nutritional value to predators.
2. Production cells are larger, allowing more efficient handling without being large enough to impede grazing activity.
3. Stock cells are more likely to be dormant and thus possess some form of protective covering such as an algal sheath.

A number of factors may also be responsible for the series of prey preference shown by grazers;

1. *Aulacoseira* is numerous and therefore grazers have adapted to utilising it as a food source. The cells and filamentous colonies are relatively large and non-motile, and may form an efficient source of grazing material although phytoplankton can show grazer resistance and/or growth enhancement in response to predation. This would reduce grazing efficiency and result in further grazer adaptation (Carrick *et al* 1991). *Aulacoseira* does not possess 'anti-grazer' structures such as spines or an algal sheath which are found in other genera (McNaught *et al* 1980) such as *Staurastrum* and *Navicula* respectively.

2. As well as being small and unicellular, flagellates are motile (some are themselves heterotrophic) and thus may actively avoid predation, making them a relatively inefficient source of nutrition. Migration patterns opposite to those of zooplankton may also aid avoidance of predation (Jones 1993), and there are differences in zooplankton feeding effects as flagellates are suppressed by daphnids but not by copepods (Jürgens & Stolpe 1995).

3. Genera such as *Microcystis* consisting of colonies of small cells are the most common form of cyanobacteria found in Lake Naivasha and again may be a relatively inefficient food source. The colonies also form a mucous matrix which may prevent digestion as seen in *Microcystis* (Porter 1977). Such organisms are capable of secreting toxins which may render them unpalatable as well as being inefficient food items due to nutritional and handling factors (Porter & Orcutt 1980).

For instance, cyanobacteria produce numerous toxins such as microcystin, anatoxin and saxitoxin although both toxic and non-toxic strains can live in the same lake. Zooplankton which consume toxic cells either die or show reduced growth, therefore they often avoid cyanobacteria, apparently by taste recognition (DeMott & Moxter 1991). Alternatively, copepods and cladocerans can sift a mixture of cells and particles,

mechanically rejecting those that are toxic. Such action may reduce the feeding rate, therefore in a system containing abundant palatable food in the form of *Aulacoseira* it may be more efficient to avoid as many cyanobacteria as possible. This is partly because although zooplankton can not handle large colonies of cyanobacteria, neither do they interfere with the filtering process.

Small colonies may however inhibit the feeding process by direct mechanical interference, with larger cladocerans generally being more affected than copepods, rotifers or *Bosmina* (Lampert 1987). This inhibition may be reduced in Naivasha because the effect is largely due to filamentous forms whilst most Naivasha cyanobacteria are globular forms such as *Microcystis* colonies, and there may also be species-specific effects. Considering zooplankton species identified in Lake Naivasha, *Microcystis* is poorly assimilated by *Daphnia longispina* and *D. magna* (Schindler 1971), although *D. hyalina* can assimilate it as well as preferred food such as *Chlorella* (DeBernardi *et al* 1981). Similarly, the rotifer *Brachionus calcyiflorus* is not affected by the presence of cyanobacteria (Starkweather & Kellar 1983). In summary, the toxicity, handling and mucous characteristics of cyanobacteria mean that they form an inadequate food source both by being individually protected and by creating an unfavourable environment for efficient grazers such as *Daphnia*.

7.4 Levels of productivity

Time series of productivity profiles have shown that daily variations in productivity could be as large as longer-term changes. High productivity was sometimes due to short-term wind-driven accumulation of productive cells (Webster & Hutchinson 1994). These results indicate that events causing high productivity could be localised and temporary, and thus not important in whole lake terms. This conclusion is supported by longer-term trends showing a more stable system not following the effects of short-term perturbations. Variations over time occurred in absolute productivity as the ratios of productivity at different depths showed no significant changes, indicating that

productivity is controlled equally at all depths. Such vertical homogeneity in productivity control may be explained as follows;

1. Variations in light intensity had a similar proportional effect upon the whole water column, although light attenuation is not linear. At or near the surface, the extent of photoinhibition varied according to differences in light intensity.

2. Lake Naivasha is well-mixed, and so variations in chemical factors generally showed little vertical heterogeneity in the water column. Exceptions occurred where productivity was high, leading to reduced nutrient levels and increased dissolved oxygen in a narrow vertical band (at approximately 0.5m depth). Where water was deeper, temporary stratification formed with associated deoxygenation, nutrient release and accumulation.

If necessary for future work, production can be predicted from Chl *a* measurements which may be useful as pigment determinations are faster and easier to make in large numbers if required. There is however error involved in using such a calibration and thus productivity measurements were made directly. In the Main lake, a productivity peak was associated with increased nutrient inflow following heavy “El Niño” rains, marked by high *Aulacoseira* levels. Increases in overall algal numbers were primarily due to increases in *Aulacoseira*, therefore this genus is the major contributor to overall productivity. Light regime is however confirmed as the dominant controlling factor by the changes in *Aulacoseira* response during suboptimal productivity. In Naivasha the meroplanktonic lifestyle occurs in genera such as *Aulacoseira* (Round 1981), but there is no productivity at the lake bed due to light attenuation and thus these cells are lost. If the benthos (probably diatoms other than *Aulacoseira*) became productive due to an environmental change such as decreased turbidity, overall productivity might rise appreciably. Productivity contributions of algal size fractions indicated that larger, less numerous, slower-acting algae contributed less than smaller, more numerous, faster-acting forms. Although *Aulacoseira* forms colonies exceeding the 65 μm threshold for consideration as a ‘large’ alga, individual cells are small (approximately 20 μm long) and thin (approximately 5 μm diameter) and easily pass through filters of this size.

7.5 Controls on productivity

Lake Naivasha is currently moderately eutrophic (Harper *et al* 1993) and the processes increasing nutrient levels also cause standard effects of eutrophication such as reduction of transparency and diversity. With recent surveys (ILEC/Lake Biwa Research Institute 1988-1993) indicating that in Africa, 28% of lakes are eutrophic (rising to 41% for South America and 54% in the Asia Pacific region), the condition and functioning of tropical freshwater ecosystems is of considerable interest and concern. Controls on primary productivity in Lake Naivasha and other shallow tropical freshwaters can be discussed with reference to the numbered hypotheses introduced in section 1.8. There are also some factors which do not appear to impose a significant control on productivity and are not covered directly by these hypotheses:

- i. Minor nutrients are found and required in low concentrations and do not appear to be limiting.
- ii. None of the background chemical factors measured vary in relation to either productivity or community composition.

Although minor nutrients and background chemicals are not found to be limiting, they may be depleted by primary producers as is the case with silicate levels during periods of high diatom production.

There are, however, a number of effective factors controlling productivity, which can be extrapolated to other shallow tropical freshwaters if conditions in the local aquatic environment are known. Such conditions are measured as the chemical, biological and hydrological parameters investigated during this study. Such parameters are generally relatively straightforward to measure given the facilities available in many developing nations, and form the bases of many ongoing monitoring programmes. The resulting

information allows controls on lake-wide primary productivity to be explained by revisiting the original hypotheses as previously numbered (Section 1.8, page 41);

1. There is nutrient limitation by both nitrogen and phosphorus with nitrogen more limiting than phosphorus. This may be due to differential nutrient limitation between component species of the planktonic community as noted by Titman (1976).

2. In general, the Naivasha phytoplankton preferentially utilise ammonium ions over nitrate ions as a source of nitrogen.

3. The lake is generally fully mixed. However, Crescent Island lagoon shows some temporary stratification with an oxycline between 0.5 and 1m depth, although it may be well-mixed to 3m depth with only incomplete stratification which is broken by wind action and convection. This means that epilimnetic nutrient depletion is also incomplete. It is however permanently stratified below approximately 10m depth and phosphorus release occurs at depth due to deoxygenation. As only the deeper, sheltered site CI undergoes regular stable stratification, SRP here shows a lower concentration above 3m in the epilimnion than in the main lake or site MR. Below 3m, this situation reverses due to anoxic release of phosphates. However, this nutrient release does not appear to affect productivity either locally (as productivity is not significantly higher in Crescent Island lagoon) or in whole lake terms. In the Main lake increased nutrient levels with depth are due only to accumulation of existing water-column nutrients.

4. Alkalinity and pH show steady variations over time periods of months due to rainfall dilution effects. These do not directly affect productivity, and although there may be effects on algal community structure, there is no direct correlation.

5. The major nutrients nitrogen and phosphorus may be depleted and become limiting, although there is nutrient recycling as well as regeneration from inflow and sediment release. The major nutrient input is from river water as augmented by rainfall events and

the subsequent increased erosion and inflow, although this also has the effect of diluting the lake. Such effects are subject to a time lag of several days and are followed by underflow and in-lake circulation.

Differences between nutrient pools outweigh spatial variations. The greatest variability is seen in the contribution of the Internal pool as the other pools remain equal but variable. Under enriched nutrient conditions, the contribution of the Recycled pool is stable as it can function even with the rapid overturn of small quantities of nutrients. Recycling may release nutrients for 'general consumption' and recycled nutrients pass through cellular processes to become part of the Internal pool.

6. Generally, diel fluctuations in environmental conditions are greater than longer-term changes, leading to a situation of 'muted seasonality' with well-adapted species persisting as assemblages for many days. Daily variations in productivity can therefore be greater than longer-term changes, but only in absolute terms, as ratios between depths are constant. The only climatic parameter which appears to affect primary production directly is rainfall, although this has to be considered in whole catchment terms due to its influence on river inflow. The River Malewa also produces an underflow of cooler river water into the lake. Wind effects can also cause localised short-term periods of high productivity through the accumulation of algal cells such as *Ceratium*. This is not important in whole-lake terms, as production is merely being spatially redistributed.

7. In early succession, low sinking rates (high turbulence) and high nutrient availability favour low SA:V species such as *Aulacoseira*, whilst the opposite situation favours high SA:V species such as *Microcystis* due to their ability to both regulate buoyancy and scavenge scarce nutrients. Overall, *Aulacoseira* is the numerically and productively dominant alga and causes periods of high productivity and low diversity with overall increases in algal numbers due largely to this genus.

Cyanobacteria are potentially important in shallow lakes as counts show they may form a large proportion of the benthos, but require sufficient water transparency. Without mixing, there would be a large (77.83%) and rapid (4 - 8 hours) productivity loss by sedimentation, followed by a shift towards cyanobacterial dominance. Work by Lewis (1979) also indicates that a shift in dominance from diatoms to cyanobacteria could occur if conditions changed to those favouring high SA:V species, such as increased water-column stability. This may be especially true as nutrient levels have increased in Lake Naivasha since the last period of cyanobacterial dominance (Kalff & Watsin 1986). The benthos could however contribute to overall productivity if water transparency increased. Surface films also make no significant contribution to productivity.

Self-shading also occurs with different responses for conditions of 'low' and 'high' productivity. With low productivity, there is a more efficient productivity:chlorophyll ratio, and a shading loss of 17%, whilst for high productivity, the greater number of cells cause lower efficiency and a loss of 46%. This is opposite to grazing control which is more important with low productivity, and thus these effects are partially counterbalanced.

8. Other than rainfall, climatic parameters vary without any definite trend or relationship with productivity, whilst some are directly interlinked. The state of permanent summer therefore means that there is no true seasonality, and that interannual climatic variations become important as longer-term persistence of the algal community develops. Tropical or 'summer' conditions especially raise the relative anabolic rates of larger (low SA:V) species such as the numerically dominant *Aulacoseira*. Low SA:V species are also favoured by low sinking rates and high nutrient availability.

Large community fluctuations may however occur within a 24-hour period. Epilimnetic fluctuations are faster and greater in magnitude than those in the hypolimnion due to the

latter showing greater physical stability and a lower production rate. Processes affecting diversity are lake-wide with hypolimnetic diversity lower than that of the epilimnion. This means that although absolute abundance may vary, community structure (as the proportion of each species in the whole community) is spatially closely linked, an effect mirrored by productivity. There is also succession of form such as filament length and cells per colony as well as of actual species. During periods of high productivity and *Aulacoseira* abundance, the number of cells per colony is therefore greater and less variable.

9. Smaller (< 65 μm), more numerous, faster-acting forms are more productive than larger forms with the opposite production strategy. There is no difference between the smallest (< 20 μm) and medium (20 - 65 μm) forms, nor is there any spatial variation. Zooplankton also prefer larger 'Production' cells over smaller 'Standing-stock' cells. Smaller (< 65 μm) more numerous, faster acting cells are however more productive than the preferred larger forms.

10. Bottom-up controls are the most important, reducing productivity by at least 50% of its potential level, whilst top-down controls in the form of zooplankton grazing account for approximately 15%. As productivity increases however, this form of top-down control becomes less important. *Aulacoseira* is preferred by zooplankton grazers, and as the dominant algal genus, this allows grazing to exert secondary, but significant, top-down control on productivity despite conditions of moderate eutrophy. This appears to be a genuine preference (as opposed to *Aulacoseira* merely being taken in proportion to its abundance) as the impact of grazing is related to *Aulacoseira* cell numbers. Cyanobacteria form the least preferred food source of those tested, a factor which could reduce the importance of grazing if cyanobacteria became dominant.

11. Light effects can dominate overall due to attenuation and chlorophyll efficiency imposing an absolute limit on productivity regardless of other factors. Since there is

light-dark adaptation of phytoplankton, the rate of mixing must be low enough for cells to adapt to the light regime. As loss of productivity with depth is greater than gains due to light-adaptation, such forms must remain near the surface.

The light regime experienced by phytoplankton therefore dominates other controls as it determines the potential level of primary production. Due to photoinhibition and light attenuation, productivity is optimal between 0.25 and 0.5m depth. Due to transparency differences, the rate of light attenuation varies between sites, but at 25cm, 50% of red and green light, and 75% of blue light are lost, whilst at 50cm, these wavelengths have lost 75% and 90% respectively. Turbid conditions mean that light attenuation reduces productivity by 50% at a depth of 1m with zero productivity at 5m. The major horizontal differences in physico-chemical conditions are between the Main lake, the Malewa rivermouth area influenced by river water inflow, and Crescent Island lagoon due to its partial hydrological separation. There is however little difference in productivity between sites except for the 0.5m peak in Crescent Island lagoon which is greater than elsewhere.

12. The microbial loop is relatively unimportant as an active community of algivores is required to release carbon (Straskrbova & Simek 1993) whereas there are only small numbers of protozoa and larger zooplankton. Summer conditions and a supply of allochthonous nutrients also reduce the importance of the loop. 'Sloppy feeding' is a minor source of nutrients, especially in eutrophic conditions, and grazing impact is primarily due to larger heterotrophs such as cladocerans which outcompete protozoa for food, contributing to their reduction in number.

The microbial community of Lake Naivasha is numerically dominated by organisms with cells smaller than 5 μm (although some may form larger colonies), especially cyanobacteria such as *Microcystis*.

7.5.1 Productivity controls in other shallow tropical lakes

As one of the main aims of this study is to explain productivity controls in shallow tropical freshwaters in general it is important to consider the extent to which conclusions drawn from work at Lake Naivasha can be applied more broadly to such systems. The major parameters and processes seen in Lake Naivasha are applicable to other 'typical' shallow tropical lakes as the main features are shared as described in Section 1.1.3. Local monitoring of basic limnological parameters may then provide the data required to understand the productivity controls in a specific lake. Climatic factors are the most predictable and are of primary importance as they determine much of the hydrological and light regimes (Nicholson 1999). For instance, rainfall and evapotranspiration control river inflow and lake level, whilst wind and insolation determine water-column mixing and thus the light regime which in turn provides an over-riding control on productivity. Physical conditions are therefore broadly predictable and relate directly to the dominance and succession of major groups found in the plankton such as cyanobacteria, diatoms, chlorophytes and dinoflagellates (Lewis 1979). Similarly, the main processes determining nutrient limitation and utilisation of fractions are applicable between such lakes, along with biotically-influenced factors such as the importance of the microbial loop and impact of zooplankton grazing.

However, not all details of productivity controls can be extrapolated from those in Lake Naivasha. Local monitoring will need to provide specific information about climate, nutrient sources and sinks, water inflows and outflows, catchment land use and other relevant human activities, diversity and abundance of planktonic species, physical and chemical conditions in the water column, and basin shape. All of these parameters may potentially have a considerable impact upon primary production, but are relatively straightforward to monitor. The information gathered can then be used within the framework provided by this study to produce a lake-specific picture of the controls on primary production, and thus aid future environmental management.

7.6 Summary

1. Light effects dominate the level of productivity. The ambient light regime depends on the intensity of Incoming Solar Radiation which is attenuated by turbidity and causes surface photoinhibition. The light regime experienced by primary producers is determined by the mixing regime and causes light-dark adaptation. Self-shading reduces photosynthetic efficiency, an effect which increases with productivity and cell numbers.

2. The primary chemical control is by nitrogen and phosphorus nutrient limitation. Nitrogen is the most limiting nutrient with an algal preference for ammonium over nitrate. Water-column nutrient concentrations are affected by land use changes and lake level fluctuations, which are in turn controlled by long-term large-scale climatic processes. Nutrient resupply occurs from both sediment release and water-column recycling.

3. Zooplankton grazing exerts a secondary control with grazer preference for prey which form a more efficient food source. This develops through adaptation to predation of common prey taxa and/or ease of handling due to prey characteristics. In total, the preferred larger prey are less productive than the smaller, more numerous fraction with faster resource use.

4. 'Summer' conditions favour large, low SA:V species. These are further favoured by high levels of mixing and nutrient availability. Cyanobacteria may however still become dominant. The conditions found in tropical lakes also reduce the importance of the microbial loop.

5. Diel fluctuations in environmental conditions are more important than longer-term changes due to the lack of tropical seasonality resulting from permanent summer conditions.

7.7 Further work

The investigation of productivity controls in tropical freshwater addresses a wide range of points, and thus suggests a number of topics in which further work could prove beneficial, either by extending existing areas, or pursuing new ones which follow from this study;

Work is being undertaken in parallel which investigates nutrient sources and sinks within Lake Naivasha and its catchment, and thus considers sediment processes in greater depth. Geochemical and geohydrological work has also been undertaken to explain water balance issues, including the fresh nature of the water. These and other studies combine to give a complete description of the lake through hydrological, chemical and biological factors, especially regarding nutrient and eutrophication processes. A predictive model could be developed to allow investigation of the effects of any proposed management activity or pressure upon the system.

Such work could consider specific impacts such as expansion of water abstraction for the Ol-Karia geothermal power station, damming of the River Malewa, and irrigation and nutrient release by the expanding horticultural industry. A final test would be validation with data from other shallow tropical lakes to consider broader applicability. Such focused environmental management can then include campaigning and control via groups such as LNKG and LNRA alongside possible educational work with relevant groups such as *shamba* owners adjoining the inflowing rivers. Specific causes of planktonic succession & community fluctuation could also be investigated, possibly via PCA. Such a specific study would allow species interactions to be considered, with inclusion of links to macrobiota. This may be relevant in a system which has undergone a number of major perturbations through the introduction of non-native species. These include fish, Louisiana Red Crayfish (*Procambarus clarkii*), *Salvinia molesta* and *Eichhornia crassipes*, with their putative associated effects on native biota such as

reductions in waterfowl and aquatic invertebrates. Ongoing work investigates crayfish effects such as predation on macrophytes and macroinvertebrates, and use of *Eichhornia* for food and shelter. Monitoring of *Salvinia* is undertaken to investigate its link with nutrient levels, especially in sheltered lagoons formed by inundation of horticultural land during periods of rising lake level. The population of the weevil *Cyrtobagus salviniae* is also monitored as it is used to control invasive *Salvinia*. The fishery is based largely on the artificially-introduced species *Oreochromis leucostictus*, *Tilapia zillii* (both tilapias) and *Micropterus salmoides* (largemouth black bass) which in turn support approximately 80 species of piscivorous birds (Harper *et al* 1990). Bird surveys continue to investigate the effects of food availability on populations such as red-knobbed coot (*Fulica cristata*) which requires aquatic macrophytes and the African fish eagle (*Haliaeetus vocifer*) which feeds mainly on the fishery species. Continuation of microbiotic work could also occur through extended investigation of the tropical microbial loop, the extent of algal heterotrophy and role of bacteria.

Appendices

1. Diatoms as ecological indicators.
2. Algal species identified 1996-8.
3. Epilithic cell density.
4. Surface film counts.
5. Sediment and sediment/water algal counts.
6. Loss by sedimentation (counts/ml).
7. Succession rates.
8. Zooplankton species identified 1996-8.
9. Site CI nutrient pool productivity profiles ($\text{mgC}/\text{m}^3/\text{hr}$).
10. Phytoplankton grazing reduction.
11. River TSS; inter-month differences Sept '97 - Mar '98.
12. River Malewa data 1997.
13. Planktonic dilution series calibration.
14. Nutrient pool productivity contributions ($\text{mgC}/\text{m}^3/\text{hr}$).
15. Dissolved oxygen change profile.
16. Productivity contributions of algal size fractions.
17. Main lake productivity profiles by sampling depth.
18. Time series of Main lake productivity profiles 23/1/98 - 13/5/98.
19. Stability of productivity during incubations.

Appendix 1: Diatoms as ecological indicators.

Widespread in a range of conditions;

Achnanthes exigua

Achnanthes minutissima

Cyclotella stelligera

Diatoma ehrenbergii

Gomphonema olivaceum

Navicula capitata

Navicula lanceolata

Navicula schoenfeldii

Navicula trivialis

Neidium ampliatum

Nitzschia amphibia

Nitzschia linearis

Nitzschia palea

Nitzschia pusilla

Stauroneis anceps

Synedra capitata

Enriched electrolyte and/or nutrient (eutrophic) conditions;

Aulacoseira ambigua

Aulacoseira granulata

Aulacoseira italica

Cyclotella meneghiniana

Nitzschia acicularis

Stephanodiscus neoastraea

Surirella angusta

Moderate to enriched electrolyte and/or nutrient conditions;

Amphora ovalis

Caloneis amphisbaena

Cocconeis placentula

Cymatopleura solea

Diatoma tenuis

Encyonema prostratum

Epithemia turgida

Gomphonema augur

Moderate to enriched electrolyte and/or nutrient conditions (cont.);

Rhopalodia gibba

Synedra acus

Synedra ulna

Tryblionella apiculata

Moderate electrolyte and/or nutrient (mesotrophic) conditions;

Gomphonema truncatum

Gyrosigma attenuatum

Navicula radiosa

Nitzschia fonticola

Synedra berolinensis

Low to moderate electrolyte and/or nutrient conditions;

Encyonema minutum

Fragilaria capucina

Gomphonema acuminatum

Navicula cryptocephala

Low electrolyte and/or nutrient (oligotrophic) conditions;

Eunotia monodon

Pinnularia maior

Pinnularia viridis

Appendix 2: Algal species identified 1996-8.

Phylum Cyanophyta

Order Chroococcales (14 spp.)

- Aphanothece caldariorum* Richter
- Aphanothece ellipsoidea* Schröder
- Aphanothece nidulans* Richter
- Chlorogloea microcystoides* Geitler
- Chroococcus limneticus* Lemmermann
- Chroococcus turgidus* (Kützing) Nägeli
- Gloeotheca rupestris* (Lyngbye) Bornet
- Merismopedia convoluta* Brébisson
- Merismopedia geminata* Lagerstedt
- Merismopedia tenuissima* Lemmermann
- Microcystis aeruginosa* (Kützing) Kützing
- Microcystis biformis* (A.Braun) Rabenhorst
- Microcystis elachista* (W. & G.S.West) Starmach
- Microcystis viridis* (A.Braun) Lemmermann

Order Nostocales (=Oscillatoriales) (11 spp.)

- Anabaena sphaerica* Bornet & Flahault
- Anabaena spiroides* (Lemmermann) Elenkin
- Anabaenopsis circularis* (G.S.West) Müller
- Borzia trilocularis* Cohn
- Lyngbya epiphytica* Gardner
- Lyngbya muralis* Kützing
- Lyngbya* sp.
- Nostoc parmelioides* Kützing
- Oscillatoria jenniferi* (Hassall) Kützing
- Oscillatoria* sp.
- Spirulina subsalsa* Oersted

Phylum Chrysophyta

Order Ochromonadales (2 spp.)

- Didymochrysis paradoxa* Pascher
- Mallomonas leboimeii* Bourrelly

Phylum Chrysophyta cont.

Order Chromulinales (7 spp.)

- Chromulina pyriformis* Playfair
- Chrysococcus rufescens* Skuja
- Chrysomonas ellipsoidea* Skvortzov
- Chrysospora fenestrata* Pascher
- Epicystis peridinearum* Pascher
- Gloeochrysis pyrenigerum* Pascher
- Ochromonas viridis* Bourrelly

Phylum Bacillariophyta

Order Achnanthes (5 spp.)

- Achnanthes brevipes* Agardh
- Achnanthes exigua* Grunow
- Achnanthes inflata* Kützing
- Achnanthes minutissima* Kützing
- Diatomella hustedtii* Manguin

Order Coscinodiscales (6 spp.)

- Aulacoseira ambigua* (Grunow) Simonsen
- Aulacoseira granulata* (Ehrenberg) Simonsen
- Aulacoseira italica* (Ehrenberg) Simonsen
- Cyclotella meneghiniana* Kützing
- Cyclotella stelligera* Cleve & Grunow
- Stephanodiscus neoastraea* Håkansson & Hickel

Order Diatomales (11 spp.)

- Cocconeis placentula* Ehrenberg
- Diatoma ehrenbergii* Kützing
- Diatoma tenuis* Agardh
- Fragilaria capucina* Desmazières
- Rhoicosphenia curvata* (Kützing) Grunow
- Synedra acus* Kützing
- Synedra berolinensis* Lemmermann
- Synedra capitata* Ehrenberg
- Synedra pulchella* Kützing
- Synedra ulna* (Nitzsch) Ehrenberg
- Synedra* sp.

Phylum Bacillariophyta cont.

Order Eunotiales (2 spp.)

Eunotia denticula (Brébisson) Rabenhorst

Eunotia monodon (Gregory) W.Smith

Order Naviculales (45 spp.)

Amphora communata Grunow

Amphora ovalis Kützing

Caloneis amphisbaena (Bory) Cleve

Cymatopleura solea (Brébisson) W.Smith

Cymbella lacustris (Agardh) Cleve

Cymbella prostrata (Berkeley) Cleve

Denticula pelagica Hustedt

Denticula thermalis Kützing

Diploneis didyma (Ehrenberg) Cleve

Encyonema minutum (Hilse in Rabenhorst) D.G.Mann

Encyonema prostratum (Berkeley) Kützing

Epithemia turgida (Ehrenberg) Kützing

Gomphonema acuminatum Ehrenberg

Gomphonema augur Ehrenberg

Gomphonema truncatum (=constrictum) Ehrenberg

Gomphonema olivaceum (Hornemann) Brébisson

Gyrosigma attenuatum (Kützing) Rabenhorst

Navicula capitata Ehrenberg

Navicula cryptocephala Kützing

Navicula cuspidata Kützing

Navicula gibbula Cleve

Navicula lanceolata (C.Agardh) Kützing

Navicula pygmaea Kützing

Navicula protractoides Hustedt

Navicula radiosa Kützing

Navicula schoenfeldii Hustedt

Navicula scutelloides W.Smith

Navicula trivialis Lange-Bertalot

Navicula tuscula (Ehrenberg) Grunow

Navicula sp.

Neidium ampliatum (Ehrenberg) Krammer

Nitzschia acicularis (Kützing) W.Smith

Phylum Bacillariophyta cont.

Order Naviculales cont.

- Nitzschia amphibia* Grunow
- Nitzschia fonticola* Grunow
- Nitzschia linearis* (Agardh) W.Smith
- Nitzschia palea* (Kützing) W.Smith
- Nitzschia pusilla* Grunow
- Nitzschia* sp.
- Pinnularia maior* Ehrenberg
- Pinnularia viridis* (Nitzsch) Ehrenberg
- Rhopalodia gibba* (Ehrenberg) O.Müller
- Stauroneis anceps* Ehrenberg
- Surirella angusta* Kützing
- Surirella linearis* W.Smith
- Tryblionella apiculata* Gregory

Phylum Chlorophyta

Order Volvocales (4 spp.)

- Chlamydomonas debaryana* Gorosch
- Chlamydomonas ovalis* Pascher
- Chlorotriangulum minutum* Kufferath
- Dunaliella lateralis* Pascher & Jahoda

Order Chlorococcales (37 spp.)

- Acanthosphaera zachariasi* (Geitler) Lemmermann
- Ankistrodesmus falcatus* (Chodat) Lemmermann
- Ankistrodesmus gelifactum* (Chodat) Bourrelly
- Ankyra ancora* (G.M.Smith) Fott
- Ankyra judai* (G.M.Smith) Fott
- Botryococcus braunii* Kützing
- Botryosphaera sudetica* (Lemmermann) Chodat
- Characium ornithocephalum* A.Braun
- Chlorella miniata* (Nägeli) Oltmanns
- Chlorella vulgaris* Beijerinck
- Chlorococcum wimmeri* (Rabenhorst) Starr
- Chodatella ciliata* (Lagerheim) Lemmermann
- Chodatella quadriseta* Lemmermann
- Coelastrum microsporum* Nägeli
- Coelastrum reticulatum* (Dangeard) Senn

Phylum Chlorophyta cont.

Order Chlorococcales cont.

- Crucigenia quadrata* Morren
- Crucigenia tetrapedia* (Korchikoff) Bourrelly
- Dictyosphaerum pulchellum* Wood
- Euastropsis richteri* (Schmidle) Lagerheim
- Micractinium pusillum* (Lund) Fresenius
- Oocystidium ovale* Korchikoff
- Oocystis lacustris* Chodat
- Pediastrum boryanum* Meyer
- Pediastrum clathratum* (Schröder) Lemmermann
- Pediastrum duplex* Meyer
- Pediastrum tetras* (Corda) Rabenhorst
- Selenastrum bibraianum* Reinsch
- Scenedesmus crassus* Chodat
- Scenedesmus falcatus* Chodat
- Scenedesmus flexuosus* (Lemmermann) Ahlstrom
- Scenedesmus protuberans* Fritsch & Rich
- Scenedesmus tenuispina* Chodat
- Scenedesmus* sp.
- Sphaerocystis schroeteri* Chodat
- Tetraedron caudatum* Lemmermann
- Tetraedron limneticum* (Skuja) Borge
- Tetrastrum heteracanthum* (Nordstedt) Chodat

Order Oedogoniales (3 spp.)

- Oedogonium mammiferum* Wittrock
- Oedogonium minus* Wittrock
- Oedogonium sudanense* Gautlièvre

Order Desmidiales (11 spp.)

- Closterium acerosum* (Schrank) Ehrenberg
- Closterium acutum* Brébisson
- Closterium setaceum* Grönblad
- Cosmarium depressum* Riverdin
- Cosmarium meneghinii* Brébisson
- Gonatozygon monotaenium* De Bary
- Micrasterias tropica* Nordstedt

Phylum Chlorophyta cont.

Order Desmidiaceae cont.

- Pleurodiscus africanus* Bourrelly
- Staurastrum lunatum* Ralfs
- Staurastrum sebaldi* Krieger & Bourrelly
- Staurodesmus dickei* (Ralfs) Lillieroth

Phylum Euglenophyta

Order Euglenales (7 spp.)

- Euglena polymorpha* Dangeard
- Euglena variabilis* Klebs
- Euglena viridis* Ehrenberg
- Phacus tortus* (Lemmermann) Swirenko
- Scytomonas pusillus* Stein
- Sphenomonas quadrangularis* Stein
- Strombomonas gibberosa* (Playfair) Deflandre

Phylum Pyrrophyta

Order Prorocentrales (2 sp.)

- Gymnodinium inversum* Nygaard
- Gymnodinium* sp.

Order Peridinales (4 spp.)

- Ceratium cornutum* (Ehrenberg) Chapman & Bachmann
- Ceratium hirundinella* (O.F.Müller) Schrank
- Peridiniopsis borgei* Lemmermann
- Peridinium volzii* Lemmermann

Order Cryptomonadales (7 spp.)

- Chroomonas acuta* Ütermohl
- Chroomonas minuta* Skuja
- Chroomonas rubra* Geitler
- Cryptomonas marssonii* Skuja
- Cryptomonas ovata* Ehrenberg
- Cryptomonas tetrapyrenoidosa* Skuja
- Tetragonidium verrucatum* Pascher

Appendix 3: Epilithic cell density.

Epilithic counts (no/mm ²)	Site & Depth (m)						
	Bay 0.25	HP 0.5	HP 3	HP 1	HP 0.25	HP 2	Bay 0
<i>Achnanthes</i>	216	152	24	96	72	32	536
<i>Amphora</i>	0	16	0	24	0	24	0
<i>Ankistrodesmus</i>	0	0	0	0	16	0	16
<i>Aulac</i> colonies	128	120	80	360	112	152	200
<i>Aulacoseira</i> cells	624	560	336	1648	576	816	816
Blue-greens	104	272	4	64	56	64	80
<i>Caloneis</i>	0	16	0	16	0	0	0
<i>Chlorella</i>	32	40	0	232	64	56	56
<i>Closterium</i>	0	0	0	0	32	40	0
<i>Coelastrum</i>	0	0	0	0	0	0	16
<i>Cosmarium</i>	0	0	0	4	16	24	0
<i>Crucigenia</i>	0	0	0	0	0	32	0
<i>Cyclotella</i>	16	12	0	24	0	0	0
<i>Cymbella</i>	48	64	0	32	24	16	104
<i>Encyonema</i>	88	48	0	16	0	0	0
<i>Epithemia</i>	16	0	12	8	0	8	4
<i>Eunotia</i>	32	0	0	0	0	0	0
Filaments	776	1040	296	256	152	32	1056
Flagellates	8	32	88	288	696	256	240
<i>Fragilaria</i>	0	0	0	0	0	0	40
<i>Gomphonema</i>	272	360	0	120	160	120	288
<i>Gonatozygon</i>	24	8	0	16	4	16	0
<i>Mastogloia</i>	16	24	0	0	0	0	0
Microzooplankton	32	72	32	56	64	104	96
<i>Navicula</i>	1128	1248	272	568	384	216	1992
<i>Nitzschia</i>	72	0	0	48	24	0	8
<i>Pediastrum</i>	0	0	0	0	0	16	0
<i>Pinnularia</i>	104	96	8	16	8	0	104
<i>Scenedesmus</i>	8	8	0	8	40	8	32
<i>Surirella</i>	16	0	32	0	0	0	0
<i>Synedra</i>	672	488	200	176	120	144	168
<i>Tetraedron</i>	0	0	0	40	0	0	0

Appendix 4: Surface film counts.

Units are counts/ml	Site					
	Bay	Bay	MR	MR	MR	Bay
<i>Achnanthes</i>	24	24	0	0	0	4
<i>Amphora</i>	20	0	0	0	0	0
<i>Ankyra</i>	0	0	32	16	4	8
<i>Aulacoseira</i> colonies	752	288	72	360	112	72
<i>Aulacoseira</i> cells	5760	1632	448	1872	624	304
Blue-greens	144	80	104	272	168	80
<i>Ceratium</i>	48	0	12	24	1664	56
<i>Characium</i>	0	0	56	0	0	0
<i>Chlorella</i>	168	40	304	20	56	12
<i>Closterium</i>	32	120	0	4	0	0
<i>Coelastrum</i>	16	0	0	0	0	0
<i>Crucigenia</i>	0	0	16	0	0	8
<i>Cyclotella</i>	64	48	8	0	0	0
<i>Cymbella</i>	4	16	96	24	0	16
<i>Encyonema</i>	0	0	48	0	0	8
<i>Epithemia</i>	40	48	4	0	0	0
Flagellates	56	120	800	448	208	72
<i>Gomphonema</i>	0	24	0	4	32	16
<i>Gonatozygon</i>	0	0	0	12	0	0
<i>Gyrosigma</i>	40	0	0	0	0	0
Microzooplankton	72	88	144	80	120	40
<i>Navicula</i>	128	176	0	56	12	32
<i>Oscillatoria</i>	0	0	12	0	0	0
<i>Pediastrum</i>	0	0	0	4	0	0
<i>Peridinium</i>	0	0	0	8	112	16
<i>Pinnularia</i>	0	32	0	0	0	0
<i>Scenedesmus</i>	28	0	0	16	0	4
<i>Staurastrum</i>	0	28	0	0	0	0
<i>Synedra</i>	192	256	280	104	24	112
<i>Tetraedron</i>	24	0	0	0	0	0

Appendix 5: Sediment and sediment/water algal counts.

Taxon	Sediment (cm ⁻²)	Sed/wat (ml ⁻¹)	Taxon	Sediment (cm ⁻²)	Sed/wat (ml ⁻¹)
<i>Achnanthes</i>	68.07	22	<i>Eunotia</i>	2.84	2
<i>Amphora</i>	2.84	4	Flagellates	192.87	128
<i>Ankistrodesmus</i>	36.87	16	<i>Fragilaria</i>	0.00	0
<i>Ankyra</i>	0.00	0	<i>Gomphonema</i>	119.12	36
<i>Aulacoseira</i> colonies	323.33	140	<i>Gonatozygon</i>	79.42	44
<i>Aulacoseira</i> cells	2418.19	1220.5	<i>Gyrosigma</i>	0.00	0
Blue-greens	192.87	208	<i>Lyngbya</i>	0.00	0
<i>Botryococcus</i>	0.00	0	<i>Micractinium</i>	2.84	12
<i>Ceratium</i>	2.84	16	<i>Navicula</i>	380.06	168
<i>Characium</i>	11.35	18	<i>Nitzschia</i>	73.74	32
<i>Chlorella</i>	62.40	72	<i>Oscillatoria</i>	0.00	0
<i>Chlorococcus</i>	0.00	0	<i>Pediastrum</i>	2.84	36
<i>Closterium</i>	53.89	44	<i>Peridinium</i>	0.00	0
<i>Cocconeis</i>	96.43	20	<i>Phacus</i>	0.00	4
<i>Coelastrum</i>	2.84	2	<i>Pinnularia</i>	17.02	24
<i>Cosmarium</i>	2.84	0	<i>Rhoicosphenia</i>	0.00	2
<i>Crucigenia</i>	5.67	16	<i>Scenedesmus</i>	14.18	40
<i>Cyclotella</i>	68.07	24	<i>Spirulina</i>	0.00	0
<i>Cymbella</i>	2.84	0	<i>Staurastrum</i>	0.00	2
<i>Diatoma</i>	0.00	0	<i>Surirella</i>	2.84	0
<i>Dictyosphaerum</i>	0.00	0	<i>Synedra</i>	266.61	104
<i>Diploneis</i>	5.67	2	<i>Tetraedron</i>	8.51	12
<i>Encyonema</i>	48.22	40	<i>Tetrastrum</i>	0.00	0
<i>Epithemia</i>	2.84	0	Other Zooplankton	96.43	44
<i>Euglena</i>	0.00	0	Total algae	4344.00	2414.5

Appendix 6: Loss by sedimentation (counts/ml).

Taxon	0 hr	4 hr	% change 0-4 hrs	8 hr	% change 0-8 hrs	change 4-8 hrs	% change 4-8 hrs
<i>Amphora</i>	4.00	32.00	700.00	0.00	-100.00	-32.00	-100.00
<i>Ankistrodesmus</i>	124.00	66.00	-46.77	71.00	-42.74	5.00	7.58
<i>Ankyra</i>	46.00	26.00	-43.48	11.00	-76.09	-15.00	-57.69
<i>Aulacoseira</i> colonies	430.00	268.00	-37.67	32.00	-92.56	-236.00	-88.06
<i>Aulacoseira</i> cells	6424.00	3356.00	-47.76	440.00	-93.15	-2916.00	-86.89
Cyanobacteria	1674.00	1422.00	-15.05	714.00	-57.35	-708.00	-49.79
<i>Characium</i>	32.00	0.00	-100.00	4.00	-87.50	4.00	N/A
<i>Chlorella</i>	110.00	70.00	-36.36	10.00	-90.91	-60.00	-85.71
<i>Closterium</i>	58.00	28.00	-51.72	0.00	-100.00	-28.00	-100.00
<i>Coelastrum</i>	20.00	16.00	-20.00	5.33	-73.33	-10.67	-66.67
<i>Cosmarium</i>	24.00	9.33	-61.11	0.00	-100.00	-9.33	-100.00
<i>Crucigenia</i>	12.00	4.00	-66.67	0.00	-100.00	-4.00	-100.00
<i>Cymbella</i>	12.00	10.67	-11.11	0.00	-100.00	-10.67	-100.00
<i>Encyonema</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Epithemia</i>	31.00	10.00	-67.74	0.00	-100.00	-10.00	-100.00
Flagellates	256.00	346.00	35.16	274.00	7.03	-72.00	-20.81
<i>Fragilaria</i>	32.00	0.00	-100.00	0.00	-100.00	0.00	0.00
<i>Gomphonema</i>	8.00	16.00	100.00	5.33	-33.33	-10.67	-66.67
<i>Mallomonas</i>	29.00	60.00	106.90	50.00	72.41	-10.00	-16.67
<i>Navicula</i>	32.00	16.00	-50.00	6.00	-81.25	-10.00	-62.50
<i>Oscillatoria</i>	8.00	0.00	-100.00	0.00	-100.00	0.00	0.00
<i>Phacus</i>	16.00	16.00	0.00	8.00	-50.00	-8.00	-50.00
<i>Scenedesmus</i>	32.00	26.00	-18.75	1.00	-96.88	-25.00	-96.15
<i>Staurastrum</i>	11.00	16.00	45.45	14.00	27.27	-2.00	-12.50
<i>Synedra</i>	254.00	186.00	-26.77	102.00	-59.84	-84.00	-45.16
<i>Tetraedron</i>	10.67	9.33	-12.50	5.33	-50.00	-4.00	-42.86
Total	9259.67	5741.33	-38.00	1721.00	-81.41	-4020.33	-70.02

Appendix 7: Succession rates.

Site	Dates	No. of days	rate/day	Total S
HP0	4/12-7/12	3	0.158	0.474
HP0	7/12-8/12	1	0.559	0.559
HP0	8/12-10/12	2	0.271	0.542
HP0-OW0	10/12-12/12	2	0.19	0.38
HP0	4/12-10/12	6	0.151	0.906
CI0	12/12-6/1	25	0.055	1.375
CI3	12/12-6/1	25	0.052	1.3
CI7	12/12-6/1	25	0.027	0.675
MR0	12/12-6/1	25	0.047	1.175
CI0	6/1-16/1	10	0.062	0.62
CI1	6/1-16/1	10	0.066	0.66
CI3	6/1-16/1	10	0.067	0.67
CI7	6/1-16/1	10	0.04	0.4
MR0	6/1-16/1	10	0.178	1.78
OW0	6/1-16/1	10	0.156	1.56
RI0	6/1-16/1	10	0.116	1.16
OW0	16/1-23/1	7	0.051	0.357
OW0	23/1-24/1	1	0.176	0.176
OW0	24/1-26/1	2	0.068	0.136
OW0	26/1-28/1	2	0.021	0.042
OW0	28/1-11/2	14	0.011	0.154
OW0	16/1-11/2	26	0.008	0.208
HP0	16/1-15/2	30	0.004	0.12
HP0	15/2-16/2	1	0.549	0.549
HP1	15/2-16/2	1	0.414	0.414
OW0	11/2-18/2	7	0.06	0.42
OW0	18/2-19/2	1	0.247	0.247
HP0	16/2-21/2	5	0.063	0.315
HP0	21/2-28/2	7	0.063	0.441
HP0	28/2-2/3	2	0.13	0.26
HP0	2/3-3/3	1	0.159	0.159
HP0	3/3-4/3	1	0.781	0.781
HP0	4/3-5/3	1	1.198	1.198
HP0	5/3-6/3	1	0.177	0.177
HP0	2/3-6/3	4	0.147	0.588
MR0	10/3-20/3	10	0.044	0.44
CI0	18/3-17/4	30	0.031	0.93
CI0	17/4-12/5	25	0.035	0.875
CI1	17/4-12/5	25	0.022	0.55
CI7	17/4-12/5	25	0.027	0.675
CI0	3/10-13/10	10	0.076	0.76
CI1	3/10-13/10	10	0.018	0.18
CI3	3/10-13/10	10	0.011	0.11
CI7	3/10-13/10	10	0.029	0.29

Appendix 8: Zooplankton species identified 1996-8.

Cladocera	
Family	Species
Daphniidae	<i>Daphnia cucullata</i>
	<i>Daphnia hyalina</i>
	<i>Daphnia longispina</i>
	<i>Daphnia magna</i>
	<i>Daphnia pulex</i>
	<i>Scapholeberis mucronata</i>
Sididae	<i>Diaphanosoma brachyurum</i>
Rotifera	
Family	Species
Brachionidae	<i>Brachionus calyciflorus</i>
	<i>Brachionus rubens</i>
	<i>Keratella cochlearis</i>
	<i>Keratella quadrata</i>
	<i>Platylabus quadricornis</i>
Synchaetidae	<i>Polyarthra remata</i>
Testudinellidae	<i>Hexarthra intermedia</i>
Trichocercidae	<i>Trichocerca chattoni</i>
	<i>Trichocerca inermis</i>
	<i>Trichocerca pusilla</i>

Appendix 9: Site CI nutrient pool productivity profiles (mgC/m³/hr).

Pools	Depth		
	0 m	0.5 m	3 m
+N+P			
R	96.02	56.05	18.81
I	62.22	146.45	9.56
E	71.92	65.53	7.72
R as %	41.72	20.91	52.12
I as %	27.03	54.64	26.50
E as %	31.25	24.45	21.38
-N			
R	31.03	62.56	0.62
I	77.63	61.27	20.56
E	57.65	56.31	3.10
R as %	18.66	34.73	2.54
I as %	46.68	34.01	84.69
E as %	34.66	31.26	12.77
-P			
R	49.76	24.36	18.03
I	71.05	114.96	6.76
E	63.94	60.25	5.39
R as %	26.93	12.21	59.73
I as %	38.46	57.60	22.39
E as %	34.61	30.19	17.87

Appendix 10: Phytoplankton grazing reduction.

Grazing dilution	Mean % change			
	<i>Scenedesmus</i> production	<i>Scenedesmus</i> stock	<i>Aulacoseira</i> production	<i>Aulacoseira</i> stock
0:1 (whole)	-90.48	-46.56	-35.40	-7.72
1:3	-63.33	-37.00	-26.59	-5.92
1:1	-27.11	-16.47	-16.34	-2.26
3:1	-0.86	-9.51	-4.62	-1.72
1:0	-0.86	-4.15	-3.06	1.94
Grazing dilution	<i>Chlorella</i> production	<i>Chlorella</i> stock	Flagellates	Cyanobacteria
0:1 (whole)	-81.72	-40.04	-18.64	-10.86
1:3	-68.76	-31.27	-14.77	-9.56
1:1	-27.94	-25.99	-25.68	-2.48
3:1	-11.67	-8.49	13.52	-2.34
1:0	5.78	3.26	-0.71	2.59

Appendix 11: River TSS; inter-month differences Sept '97 - Mar '98.

Chi ² p-values	Sep vs Oct	Sep vs Nov	Sep vs Jan	Sep vs Feb	Sep vs Mar
Malewa	0.999947	0.993839	0.98298	0.998777	0.999675
Karati	0.767899	0.973296	0.983198	0.927498	0.89673
Gilgil	0.960738	0.05283	0.555568	0.472107	0.974925
Bold = SIG	Oct vs Nov	Oct vs Jan	Oct vs Feb	Oct vs Mar	Nov vs Jan
Malewa	0.997746	0.805126	0.980216	0.956251	0.948432
Karati	0.0065	0.0221	0.725484	0.0025	0.995382
Gilgil	0.361239	0.900343	0.98344	0.957045	0.0002
	Nov vs Feb	Nov vs Mar	Jan vs Feb	Jan vs Mar	Feb vs Mar
Malewa	0.55228	0.0022	0.985715	0.428785	0.999104
Karati	0.98073	0.996184	0.997558	0.999984	0.664844
Gilgil	1 x 10⁻³⁸	4 x 10⁻³³	0.685576	0.717558	0.899519

All significant differences are **reductions** over time.

No significant inter-river differences.

Appendix 12: River Malewa data 1997.

Month	Temp (°C)	Cond (µS/cm)	TDS (mg/l)	pH
July	14.9	72.4	36.4	8.08
Aug	14.7	56.9	28.3	-
Sept	16.7	91	46	9.45
Oct	18.4	53.2	26.7	7.05
Nov	16.8	79.8	39.9	7.12
Month	Alkalinity (mg/l as CaCO ₃)	Total Hardness	Calcium (mg/l as CaCO ₃)	Magnesium (mg/l)
July	36	22.8	-	-
Aug	30	13.6	-	-
Sept	104	34	18	16
Oct	10	12	14	10
Nov	28	28	12	16
Month	NH ₄ ⁺ (µg/l)	NO ₃ ⁻ (µg/l)	TN (mg/l)	
July	140	120	1.4	
Aug	150	110	-	
Sept	80.5	230	0.6	
Oct	15	210	0.65	
Nov	<0	180	2.5	
Month	SRP (µg/l)	TP (µg/l)	Iron (mg/l)	
July	160	-	0.05	
Aug	140	-	0.76	
Sept	38.1	63.3	0.46	
Oct	23.6	105.83	0.49	
Nov	49.6	128.2	1.46	

Appendix 13: Planktonic dilution series calibration.

% whole lake water	% remaining per taxon
100	100
75	87.14
50	50.28
25	20.62
20	15.87
12.5	11.55
10	9.52
6.25	4.82
0	0

Appendix 14: Nutrient pool productivity contributions (mgC/m³/hr).

Site MR	Productivity contribution		
	+N+P	-N	-P
R	55.97	72.77	74.23
I	105.87	3.69	16.74
E	56.97	53.83	63.34
R as %	25.58	55.85	48.10
I as %	48.38	2.83	10.85
E as %	26.04	41.32	41.05
Site CI	+N+P	-N	-P
R	90.43	51.46	54.59
I	81.16	45.70	51.80
E	68.65	58.65	65.89
R as %	37.70	33.09	31.74
I as %	33.65	29.11	29.64
E as %	28.66	37.80	38.62
Main lake	+N+P	-N	-P
R	64.92	65.31	71.95
I	113.08	22.27	46.69
E	63.16	57.57	61.94
R as %	27.38	44.40	40.09
I as %	46.26	15.74	25.24
E as %	26.35	39.86	34.67

Appendix 15: Dissolved oxygen change profile.

Profile section	Change in dO concentration (mg l ⁻¹ m ⁻¹)		
	Site CI	Site MR	Main lake
0m - 0.25m	0.81	0.36	0.61
0.25m - 0.5m	0.20	-0.40	-0.02
0.5m - 1m	-1.49	-0.54	-0.50
1m - 2m	-0.60	-0.15	-0.39
2m - 3m	-0.78		-0.31
3m - 5m	-0.42		-0.06
5m - 7m	-0.32		

Appendix 16: Productivity contributions of algal size fractions.

Fraction	% Contribution to productivity			
	Main	CI	MR	Mean
A	35.45	43.49	40.00	39.65
C	20.55	20.70	23.52	21.59
D	44.01	35.81	36.48	38.77
Fraction	0m	0.5m	3m	Mean
A	38.76	32.64	37.22	36.21
C	24.76	26.89	27.19	26.28
D	36.49	40.47	35.60	37.52

Appendix 17: Main lake productivity profiles by sampling depth.

Depth (m)	Mean productivity by sample depth (mgC/m ³ /hr)				
	0m	0.25m	0.5m	1m	3m
0	124.39	113.40	112.36	106.14	97.07
0.25	144.80	159.58	151.61	140.57	126.85
0.5	109.02	124.38	118.91	123.37	133.05
0.75	83.48	94.41	99.54	94.60	106.68
1	58.73	67.55	68.94	75.38	87.59
1.5	50.77	54.64	57.11	58.72	71.85
2	30.40	29.05	31.83	36.03	41.42
3	14.87	14.44	18.69	21.12	25.90

Appendix 18: Time series of Main lake productivity profiles 23/1/98 - 13/5/98.

Depth (m)	Productivity by date (mgC/m ³ /hr)				
	23/1	14/2	15/2	16/2	17/2
0	168.95	149.62	138.82	135.39	118.51
0.25	180.13	159.75	203.1	180.61	161.39
0.5	127.44	118.93	127.48	109.88	127.06
1	78.13	52.21	74.96	83.07	63.21
3	40.4	37.66	20.15	34.94	31.98
5	0	0	0	0	0
Depth (m)	17/4	8/5	9/5	10/5	13/5
0	112.84	98.93	89.42	102.76	106.23
0.25	157.18	131.45	122.83	142.53	157.03
0.5	125.29	117.91	101.77	120.79	139.27
1	87.84	85.31	85.35	80.22	98.61
3	22.77	17.56	16.75	17.07	18.09
5	0	0	0	0	0

Appendix 19: Stability of productivity during incubations.

Incubation time (hr)	Productivity (mgC/m ³ /hr)		
0.5	250.00	328.13	312.50
0.75	187.50	229.17	270.84
1	156.25	171.88	210.94
1.5	104.69	135.42	156.25
2	95.70	101.56	146.48
2.5	89.06	100.00	148.44
3	91.15	101.56	154.95
3.5	89.29	99.34	154.03
4	87.89	99.61	152.34
4.5	88.54	100.69	145.82
5	75.63	92.19	143.75
6	82.86	83.98	114.58
6.5	N/A	76.92	134.62
7	84.82	70.31	101.56
8	66.40	59.08	121.09

Linear sections are indicated by bold type.

References

Andersen, T., Schartau, A.K.L. & Paasche, E. (1991). Quantifying external and internal nitrogen and phosphorus pools, as well as nitrogen and phosphorus supplied through remineralisation, in coastal marine plankton by means of a dilution technique. *Marine Ecology Progress Series* **69**: 67-80.

AOAC (1955). *Official Methods of Analysis, 8th edition* Method 2.28, p. 13. Association of Official Agricultural Chemists, Washington DC.

Ase, L.E. (1987). A note on the water budget of Lake Naivasha, Kenya - especially the role of *Salvinia molesta* Mitch. and *Cyperus papyrus* L. *Geografiska Annaler* **69A**: 415-29.

Ase, L.E., Sernbo, K. & Syren, P. (1986). Studies of Lake Naivasha, Kenya, and its drainage area. *Naturgeografiska Institutionen Stockholms Universitet, Forsningsrapport* **63**: 1-75.

Azam, F., Fenchel, T., Field, J.G., Gray, J.S., Meyer-Reil, L.A. & Thingstad, F. (1983). The Ecological role of Water-column Microbes in the Sea. *Marine Ecology Progress Series* **10**: 257-263.

Baykov, A.A., Evtushenko, O.A. & Avaeva, S.M. (1988). A Malachite Green Procedure for Orthophosphate Determination and Its Use in Alkaline Phosphatase-Based Enzyme Immunoassay. *Analytical Biochemistry* **171**: 266-70.

Beadle, L.C. (1974). *The inland waters of tropical Africa*. Longman, London.

Boudreau, B.P. & Guinasso, N.L. (1982). The influence of a diffusive sublayer on accretion, dissolution and diagenesis at the sea floor. In: *The Dynamic Environment of the Ocean Floor*, eds K.A.Fanning & F.T.Mannheim. Bernal Books, Lexington.

Burgis, M.J., Darlington, J.P., Dunn, I.G., Ganf, G.G., Gwahaba, J.J. & McGowan, L.M. (1973). The biomass and distribution of organisms in Lake George, Uganda. *Proceedings of the Royal Society of London B* **184**: 271-298.

Burrows, C.J. (1990). *Processes of vegetation change*. Unwin Hyman, London.

Carmouze, J.-P., Durand, J.-R. & Leveque, C. (eds) (1983). *Lake Chad: ecology and productivity of a shallow tropical ecosystem*. Dr W.Junk, The Hague.

Caron, D.A. (1994). Inorganic Nutrients, Bacteria, and the Microbial Loop. *Microbial Ecology* **28**: 295-298.

Carpenter, J.H. (1965). The accuracy of the Winkler method for dissolved oxygen analysis. *Limnology & Oceanography* **10**: 135-40.

Carpenter, S.R. (ed.) (1988). *Complex interactions in Lake Communities*. Springer-Verlag, New York.

Carrick, H.J., Fahnenstiel, G.L., Stoemer, E.F. & Wetzel, R.G. (1991). The importance of zooplankton-protozoan couplings in Lake Michigan. *Limnology & Oceanography* **36**(7): 1335-1345.

Chorus, I. & Bartram, J. (1999). *Toxic cyanobacteria in water*. E & FN Spon, London.

Clark, F. (1992). A study of a population of *Micronecta scutellaris* Stal (Hemiptera: Corixidae) in Lake Naivasha, Kenya. *Hydrobiologia* **248**: 115-124.

Clymo, R.S. (1995). Nutrients and limiting factors. *Hydrobiologia* **315**: 15-24.

Cogels, F-X. & Gac, J.Y. (1993). Evaporation and annual evolution of chloride concentrations in the water of a shallow Sahelian lake: Lake of Guiers (Senegal). *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**: 115-8.

Cox, E.J. (1996). *Identification of Freshwater Diatoms from Live Material*. Chapman & Hall, London.

DeBernardi, R., Giussani, G. & Lasso-Pedretti, E. (1981). The significance of blue-green algae as food for filter-feeding zooplankton: experimental studies on *Daphnia* spp. fed by *Microcystis aeruginosa*. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **21**: 477-83.

del Giorgio, P.A. & Peters, R.H. (1994). Patterns in planktonic P:R ratios in lakes: Influence of lake trophicity and dissolved organic carbon. *Limnology & Oceanography* **39**(4): 772-787.

DeMott, W.R. & Moxter, F. (1991). Foraging on cyanobacteria by copepods: responses to chemical defenses and resource abundance. *Ecology* **72**: 1820-34.

Dugdale, R.C. & Goering, J.J. (1967). Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology & Oceanography* **12**:196-206.

Dumont, H.J. (1980). Zooplankton and the science of Biogeography: The example of Africa. In: Kerfoot (1980).

Eisenreich, S.J., Bannerman, R.T. & Armstrong, D.E. (1975). A simplified phosphorus analysis technique. *Environmental Letters* **9**: 43-53.

Elser, J.J. & Frees, D.L. (1995). Microconsumer grazing and sources of limiting nutrients for phytoplankton growth. *Limnology & Oceanography* **40**: 1-16.

Foree, E.G., Jewell, W.J. & McCarty, P.L. (1971). The extent of nitrogen and phosphorus regeneration from decomposing algae. In: *Proceedings of the 5th International Conference on Advances in Water Pollution Research* **2**.

Ganf, G.G. (1970). The regulation of net primary production in Lake George, Uganda, East Africa. *Proceedings of the IBP-UNESCO Symposium on productivity problems of Freshwaters*.

Ganf, G.G. (1974a). Incident solar irradiance and underwater light penetration as factors controlling the chlorophyll *a* content of a shallow equatorial lake (Lake George, Uganda). *Journal of Ecology* **62**: 593-609.

Ganf, G.G. (1974b). Diurnal mixing and the vertical distribution of phytoplankton in a shallow equatorial lake (Lake George, Uganda). *Journal of Ecology* **62**: 611-629.

Ganf, G.G. (1975). Photosynthetic production and irradiance-photosynthesis relationships of the phytoplankton from a shallow equatorial lake (Lake George, Uganda). *Oecologia* **16**: 165-83.

- Ganf, G.G. & Horne, A.J. (1975). Diurnal stratification, photosynthesis and nitrogen-fixation in a shallow, equatorial lake (Lake George, Uganda). *Freshwater Biology* **5**: 13-39.
- Ganf, G.G. & Viner, A.B. (1973). Ecological stability in a shallow equatorial lake (L. George, Uganda). *Proceedings of the Royal Society B* **184**: 321-46.
- Gaudet, J.J. & Melack, J.M. (1981). Major ion chemistry in a tropical African lake basin. *Freshwater Biology* **11**: 309-33.
- Gerritsen, J. (1980). Adaptive Responses to Encounter Problems. In: Kerfoot (1980).
- Gibson, C.E. (1975). Cyclomorphosis in natural populations of *Oscillatoria redekei* Van Goor. *Freshwater Biology* **5**: 279-86.
- Gibson, C.E. & Guillot, J. (1997). Sedimentation in a large lake: the importance of fluctuations in water level. *Freshwater Biology* **37**: 597-604.
- Gillbricht, R. (1952). Untersuchungen zur Produktionsbiologie des Planktons in der Kieler Bucht. Teil I. *Kieler Meeresforsch* **8(2)**: 173-91.
- Giller, P.S., Hildrew, A.G. & Raffaelli, D.G. (eds) (1992). *Aquatic Ecology. Scale, Pattern and Process*. Blackwell Science, Oxford.
- Goldberg, D.E. & Estabrook, G.F. (1998). Separating the effects of number of individuals sampled and competition on species diversity: an experimental and analytic approach. *Journal of Ecology* **86**: 983-8.
- Goldman, C.R. & Horne, A.J. (1983). *Limnology*. McGraw-Hill, London.
- Greenwood, P.H. (1976). Lake George, Uganda. *Philosophical Transactions of the Royal Society of London B* **274**: 375-391.
- Gulati, R.D., Martinez, C.P. & Siewertsen, K. (1995). Zooplankton as a compound mineralising and synthesising system: phosphorus excretion. *Hydrobiologia* **315**: 25-37.

Hansen, A-M., Andersen, F.Ø. & Jensen, H.S. (1997). Seasonal pattern in nutrient limitation and grazing control of the phytoplankton community in a non-stratified lake. *Freshwater Biology* **37**: 523-34.

Harper, D.M., Mavuti, K.M. & Muchiri, S.M. (1990). Ecology and Management of Lake Naivasha, Kenya, in Relation to Climatic Change, Alien Species' Introductions, and Agricultural Development. *Environmental Conservation* **17** (4): 328-36.

Harper, D.M. (1991). Primary Production in Lake Naivasha, Kenya. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **24**: 1112-1116.

Harper, D.M. (1992a). The ecological relationships of aquatic plants at Lake Naivasha, Kenya. *Hydrobiologia* **232**: 65-71.

Harper, D.M. (1992b). *Eutrophication of Freshwaters. Principles, problems and restoration*. Chapman & Hall, London.

Harper, D.M., Adams, C. & Mavuti, K. (1995). The aquatic plant communities of the Lake Naivasha wetland, Kenya: pattern, dynamics and conservation. *Wetlands Ecology and Management* **3** (2): 111-123.

Harper, D.M. & Mavuti, K. (1995). Freshwater wetlands and marshes. In: *Freshwater Wetlands and Marshes in Ecosystems of East Africa and their Conservation*, eds T.R. McClanahan & T. Young, Oxford University Press, Oxford.

Harper, D.M., Phillips, G., Chilvers, A., Kitaka, N. & Mavuti, K. (1993). Eutrophication prognosis for Lake Naivasha, Kenya. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**: 861-865.

Harris, G.P. (1983). Mixed layer physics and phytoplankton populations; studies in equilibrium and non-equilibrium ecology. *Proceedings of Phycological Research* **2**: 1-52.

Harris, G.P. (1994a). Pattern, process and prediction in aquatic ecology. A limnological view of some general ecological problems. *Freshwater Biology* **32**: 143-160.

- Harris, G.P. (1994b). *Phytoplankton Ecology. Structure, Function and Fluctuation*. Chapman & Hall, London.
- Harris, G.P. & Baxter, G. (1996). Interannual variability in phytoplankton biomass and species composition in a subtropical reservoir. *Freshwater Biology* **35**: 545-560.
- Hartley, A.M., House, W.A., Callow, M.E. & Leadbeater, B.S.C. (1995). The role of a green alga in the precipitation of calcite and the coprecipitation of phosphate in freshwater. *Internationale revue der gesamten Hydrobiologie* **80**: 385-401.
- Havilah, E.J., Wallis, D.M., Morris, R. & Woolnough, J.A. (1977). A microcolorimetric method for determination of ammonia in Kjeldahl digests with a manual spectrophotometer. *Laboratory Practice* **26**: 545-7.
- Hawkes, H.A. (1979). Invertebrates as indicators of river quality. In: *Biological Indicators of Water Quality*, eds A.James & L.Evison. Wiley, Chichester.
- Heaney, S.I., Parker, J.E., Butterwick, C. & Clarke, K.J. (1996). Interannual variability of algal populations and their influence on lake metabolism. *Freshwater Biology* **35**: 561-577.
- Hellebust, J.A. (1965). Excretion of some organic compounds by marine phytoplankton. *Limnology & Oceanography* **10**: 192-206.
- Hessen, D.O., Andersen, T. & Faafeng, B. (1992). Zooplankton contribution to particulate phosphorus and nitrogen in lakes. *Journal of Plankton Research* **14**(7): 937-947.
- Hessen, D.O. & Andersen, T. (1992). The algae-grazer interface: feedback mechanisms linked to elemental ratios and nutrient cycling. *Ergebnisse der Limnologie* **35**: 111-120.
- HMSO (1980). *The determination of Chlorophyll a in aquatic environments 1980 (revision)*. HMSO, London.
- Hobbie, J.E., Daley, R.J. & Jasper, S. (1977). Use of Nuclepore Filters for Counting Bacteria by Fluorescence Microscopy. *Applied and Environmental Microbiology* **33**: 1225-1228.
- Holm-Hansen, O. (1969). Environmental and nutritional requirements for Algae. *Proceedings of the Eutrophication-Biostimulation Assessment Workshop* **1**: 19-21.

Huatuco, L.D.H. (1998). *Water availability assessment using multi-objective decision support systems (MODSS): A study around Lake Naivasha, Rift Valley Province, Kenya*. MSc thesis, ITC, Netherlands.

Hubble, D.S. (1996). *Monitoring of Chalk Grassland Re-creation*. MSc thesis, Cranfield University, UK.

Hutchinson, G.E. (1967). *A treatise on Limnology. Vol II. Introduction to lake biology and the limnoplankton*. J.Wiley & Sons, Chichester.

ILEC/Lake Biwa Research Institute (1988-1993). *Survey of the State of the World's Lakes*. International Lake Environment Committee, Otsu & United Nations Environment Programme, Nairobi.

Jassby, A.D. & Goldman, C.R. (1974). A quantitative measure of succession rate and its application to the phytoplankton of lakes. *American Naturalist* **108**: 688-93.

Jones, B.F. & Bowser, C.J. (1978). The Mineralogy and related chemistry of lake sediments. In: A.Lerman (ed.) *Lakes: Chemistry, Geology, Physics*. Springer-Verlag, New York.

Jones, R.I. (1993). Phytoplankton migrations: patterns, processes and profits. *Archiv für Hydrobiologie, Beiheft Ergebnisse der Limnologie* **39**: 67-77.

Jürgens, K. & Stolpe, G. (1995). Seasonal dynamics of crustacean zooplankton, heterotrophic nanoflagellates and bacteria in a shallow, eutrophic lake. *Freshwater Biology* **33**: 27-38.

Kalff, J. (1983). Phosphorus limitation in some tropical African lakes. *Hydrobiologia* **100**: 101-12.

Kalff, J. & Brumelis, D. (1993). Nutrient loading, wind speed and phytoplankton biomass in a tropical African lake. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**: 860.

Kalff, J. & Watson, S. (1986). Phytoplankton and its dynamics in two tropical lakes: a tropical and temperate zone comparison. *Hydrobiologia* **138**: 161-176.

Kerfoot, W.C. (ed) (1980). *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, New England.

Kilham, P. & Kilham, S.S. (1990). Endless summer: internal loading processes dominate nutrient cycling in tropical lakes. *Freshwater Biology* **23**: 379-389.

Kirk, J.T. (1994). *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge.

Kitaka, N. (1991). *Phytoplankton Productivity in Lake Naivasha*. MSc Thesis, University of Leicester.

Knighton, D. (1998). *Fluvial Forms and Processes*. Arnold, London.

Krause-Jensen, D. & Sand-Jensen, K. (1998). Light attenuation and photosynthesis of aquatic plant communities. *Limnology & Oceanography* **43**(3): 396-407.

Krömer, S. (1995). Respiration during Photosynthesis. *Annual Review of Plant Physiology* **46**: 45-70.

Lampert, W. (1987). Laboratory studies on zooplankton cyanobacteria interactions. *New Zealand Journal of Marine & Freshwater Research* **21**: 483-90.

Lande, R. (1996). Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76**: 5-13.

Landry, M.R. & Hassett, R.P. (1982). Estimating the Grazing Impact of Marine Microzooplankton. *Marine Biology* **67**: 283-288.

Landry, M.R., Kirshtein, J. & Constantinou, J. (1995). A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the central equatorial Pacific. *Marine Ecology Progress Series* **120**: 53-63.

Le Cren, E.D. & Lowe-McConnell, R.H. (1980). *The functioning of freshwater ecosystems*. Cambridge University Press, Cambridge.

Lehman, J.T. (1980). Nutrient recycling as an interface between Algae and Grazers in Freshwater Communities. In: Kerfoot (1980).

- Lewis, W.M. (1976). Analysis of succession in a tropical phytoplankton community and a new measure of succession rate. *American Naturalist* **112**: 401-14.
- Lewis, W.M. (1978a). Dynamics and succession of the phytoplankton in a tropical lake. *Journal of Ecology* **66**: 849-80.
- Lewis, W.M. (1978b). A compositional, phytogeographical and elementary structural analysis of the phytoplankton in a tropical lake: Lake Lanao, Philippines. *Journal of Ecology* **66**: 213-226.
- Lewis, W.M. (1979). *Zooplankton community analysis: studies on a tropical system*. Springer-Verlag, New York.
- Lind, E.M. (1968). Notes on the distribution of phytoplankton in some Kenya waters. *British Phycological Bulletin* **3(3)**: 481-493.
- Lobo, E.A., Katoh, K. & Aruga, Y. (1995). Response of epilithic diatom assemblages to water pollution in rivers in the Tokyo Metropolitan Area, Japan. *Freshwater Biology* **34**: 191-204.
- Long, S.P., Humphries, S. & Falkowski, P.G. (1994). Photoinhibition of Photosynthesis in Nature. *Annual Review of Plant Physiology and Plant Molecular Biology* **45**: 633-662.
- Macek, M. (1992). Distribution of ciliates in the Rimov reservoir. *Archiv für Hydrobiologie, Beiheft Ergebnisse der Limnologie* **40**: 137-141.
- Mackereth, F.J., Heron, J. & Talling, J.F. (1989). *Water Analysis*. Freshwater Biological Association, Ambleside.
- Margalef, R. (1967). Some concepts relative to the organisation of plankton. *Oceanography & Marine Biology Review* **5**: 227-89.
- Mavuti, K., Moreau, J., Munyandorero, J. & Plisnier, P.D. (1996). Analysis of trophic relationships in two shallow equatorial lakes Lake Naivasha (Kenya) and Lake Ihema (Rwanda) using a multispecific trophic model. *Hydrobiologia* **321**: 89-100.
- McNaught, D.C., Griesmer, D. & Kennedy, M. (1980). Resource characteristics modifying selective grazing by Copepods. In: Kerfoot (1980).

- Melack, J.M. (1979a). Photosynthetic rates in four tropical freshwaters. *Freshwater Biology* **9**: 555-571.
- Melack, J.M. (1979b). Temporal variability of phytoplankton in tropical lakes. *Oecologia* **44**: 1-7.
- Melack, J.M. (1988). Primary producer dynamics associated with evaporative concentration in a shallow, equatorial soda lake (Elementeita, Kenya). *Hydrobiologia* **158**: 1-14.
- Metz, K., Beattie, K.A., Codd, G.A., Hanselmann, K., Hauser, B., Naegeli, H.P. & Preisig, H.R. (1997). Identification of a microcystin in benthic cyanobacteria linked to cattle deaths in alpine pastures in Switzerland. *European Journal of Phycology* **32**: 111-117.
- Meyers, D.G. (1980). Diurnal Vertical Migration in Aquatic Microcrustacea: Light and Oxygen Responses of Littoral Zooplankton. In: Kerfoot (1980).
- Mitsch, W.J. & Gosselink, J.G. (1993). *Wetlands, 2nd edition*. Van Nostrand Reinhold, New York.
- Moss, B. (1973). The influence of environmental factors on the distribution of freshwater algae: An experimental study IV. Growth of test species in natural lakewaters and conclusion. *Journal of Ecology* **61**: 193-211.
- Moss, B. (1998). *Ecology of Fresh Waters, 3rd edition*. Blackwell Science, Oxford.
- Mugidde, R. (1993). Increase in phytoplankton primary productivity and biomass in Lake Victoria. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**: 846-849.
- Nagata, T. & Kirchman, D.L. (1992). Release of dissolved organic matter by heterotrophic protozoa: implications for microbial food webs. *Archiv für Hydrobiologie, Beiheft Ergebnisse der Limnologie* **35**: 99-109.
- Nedwell, D.B. & Brown, C.M. (1982). *Sediment Microbiology*. Academic Press, London.

Nicholson, S.E. (1999). Historical and modern fluctuations of Lakes Tanganyika and Rukwa and their relationship to rainfall variability. *Climatic Change* **44**: 53-71.

Njuguna, S.G. (1988). Nutrient-phytoplankton relationships in a tropical meromictic soda lake. *Hydrobiologia* **158**: 15-28.

Noble, I.R. & Slatyer, R.O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**: 5-21.

Olila, O.G., Reddy, K.R. & Harris, W.G. (1995). Forms and distribution of inorganic phosphorus in sediments of two shallow eutrophic lakes in Florida. *Hydrobiologia* **302**: 147-161.

Patrick, R. (1977). *Ecology of freshwater diatoms - Diatom communities*. In: Werner (1977).

Patterson, G. & Wilson, K.K. (1995). The influence of the diel climatic cycle on the depth-time distribution of phytoplankton and photosynthesis in a shallow equatorial lake (Lake Baringo, Kenya). *Hydrobiologia* **304**: 1-8.

Phlips, E.J., Aldridge, F.J., Schelske, C.L. & Crisman, T.L. (1995). Relationships between light availability, chlorophyll *a*, and tripton in a large, shallow subtropical lake. *Limnology & Oceanography* **40**: 416-421.

Poister, D., Armstrong, D.E. & Hurley, J.P. (1999). Influences of grazing on temporal patterns of algal pigments in suspended and sedimenting algae in a north temperate lake. *Canadian Journal of Fisheries & Aquatic Sciences* **56(1)**: 60-69.

Pollinger, U. (1981). The structure and dynamics of the phytoplankton assemblages in Lake Kinneret, Israel. *Journal of Plankton Research* **3(1)**: 93-105.

Porter, K.G. (1977). The plant-animal interface in freshwater ecosystems. *American Scientist* **65**: 159-70.

Porter, K.G. & Orcutt, J.D. (1980). Nutritional adequacy, manageability and toxicity as factors that determine food quality of Green and Blue-Green Algae for *Daphnia*. In: Kerfoot (1980).

Reynolds, C.S. (1984). *The Ecology of Freshwater Phytoplankton*. Cambridge University Press.

Reynolds, C.S. (1992). Dynamics, selection and composition of phytoplankton in relation to vertical structure in lakes. *Ergebnisse der Limnologie* **35**: 13-31.

Reynolds, C.S. (1996). Phosphorus recycling in lakes: evidence from large limnetic enclosures for the importance of shallow sediments. *Freshwater Biology* **35(3)**: 623-645.

Reynolds, C.S. (1997). *Vegetation Processes in the Pelagic. A Model for Ecosystem Theory*. Ecology Institute, Oldendorf/Luhe.

Reynolds, C.W., Oliver, R.L. & Walsby, A.E. (1987). Cyanobacterial dominance: the role of buoyancy regulation in dynamics lake environments. *New Zealand Journal of Marine and Freshwater Research* **21**: 491-502.

Rheinheimer, G. (1991). *Aquatic Microbiology 4th edition*. Wiley, Chichester.

Richardson, J.L. & Richardson, A.E. (1972). History of an African Rift Lake and its climatic implications. *Ecological Monographs* **42**: 499-534.

Robarts, R.D. & Zohary, T. (1987). Temperature effects on photosynthetic capacity, respiration and growth rates of bloom-forming cyanobacteria. *New Zealand Journal of Marine and Freshwater Research* **21**: 391-399.

Romo, S., van Donk, E., Gylstra, R. & Gulati, R. (1996). A multivariate analysis of phytoplankton and food web changes in a shallow biomanipulated lake. *Freshwater Biology* **36**: 683-696.

Rosén, G. (1981). Phytoplankton indicators and their relations to certain chemical and physical factors. *Limnologica* **13(2)**: 263-290.

Round, F.E. (1981). *The Ecology of Algae*. Cambridge University Press.

Round, F.E. (ed.) (1988). *Algae and the Aquatic Environment*. Biopress, Bristol.

- Salonen, K., Jones, R.I., DeHaan, H. & James, M. (1994). Radiotracer study of phosphorus uptake by plankton and redistribution in the water column of a small humic lake. *Limnology & Oceanography* **39**(1): 69-83.
- Sanders, R.W., Porter, K.G., Bennett, S.J. & DeBiase, A.E. (1989). Seasonal patterns of bacterivory by flagellates, ciliates, rotifers and cladocerans in a freshwater planktonic community. *Limnology & Oceanography* **34**(4): 673-687.
- Schindler, J.E. (1971). Food quality and zooplankton nutrition. *Journal of Animal Ecology* **40**: 589-95.
- Schreurs, H. (1992). Cyanobacterial dominance, relation to eutrophication and lake morphology. PhD thesis, University of Amsterdam.
- Serruya, C. & Pollinger, U. (1977). Lowering of water level and algal biomass in Lake Kinneret. *Hydrobiologia* **54**(1): 73-80.
- Serruya, C. & Pollinger, U. (1983). *Lakes of the Warm Belt*. Cambridge University Press.
- Shapiro, J. (1997). The role of carbon dioxide in the initiation and maintenance of blue-green dominance in lakes. *Freshwater Biology* **37**: 307-323.
- Sherr, E.B. & Sherr, B.F. (1994). Bacterivory and Herbivory: Key Roles of Phagotrophic Protists in Pelagic Food Webs. *Microbial Ecology* **28**: 223-235.
- Sherr, E.B., Sherr, B.F. & Paffenhofer, G.-A. (1986). Phagotrophic protozoa as food for metazoans: a "missing" trophic link in marine pelagic food webs? *Marine microbial food webs* **1**(2): 61-80.
- Simek, K., Macek, M., Seda, J. & Vyhnalek, V. (1990). Possible food chain relationships between bacterioplankton, protozoans and cladocerans in a reservoir. *Internationale Revue der gesamten Hydrobiologie* **75**(5): 583-596.
- Simek, K. & Straskrabova, V. (1992). Bacterioplankton production and protozoan bacterivory in a mesotrophic reservoir. *Journal of Plankton Research* **14**(6): 773-787.
- Simpson, E.H. (1949). Measurement of diversity. *Nature* **163**: 688.
- Spellerberg, I.F. (1991). *Monitoring Ecological Change*. Cambridge University Press.

Starkweather, P.L. & Kellar, P.E. (1983). Utilization of cyanobacteria by *Brachionus calcyiflorus*: *Anabaena flos-aquae* (NRC-44-1) as a sole or complementary food source. *Hydrobiologia* **104**: 373-8.

Sterner, R.W. (1990). The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *American Naturalist* **136**: 209-229.

Straskrabova, V. & Simek, K. (1993). Microbial loop in lakes and reservoirs related to trophy and metazooplankton development. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* **25**: 1183-1186.

Stumm, W. & Baccini, P. (1978). Man-made chemical perturbation of lakes. In: A.Lerman (ed.) *Lakes: Chemistry, Geology, Physics*. Springer-Verlag, New York.

Talling, J.F. (1957). The phytoplankton population as a compound photosynthetic system. *New Phytologist* **56**: 133-149.

Talling, J.F. (1966). The annual cycle of stratification and phytoplankton growth in Lake Victoria (East Africa). *Internationale revue der gesamten Hydrobiologie* **51**: 545-621.

Talling, J.F. (1993). Environmental regulation in African shallow lakes and wetlands. *Revue d'Hydrobiologie Tropicale* **25 (2)**: 87-144.

Talling, J.F. & Talling, I.B. (1965). The chemical composition of African lake waters. *Internationale revue der gesamten Hydrobiologie* **50**: 421-463.

Taylor, A.H. & Joint, I. (1990). A steady-state analysis of the microbial loop in stratified systems. *Marine Ecology Progress Series* **59**: 1-17.

Titman, D. (1976). Ecological competition between algae: Experimental confirmation of resource-based competition theory. *Science* **192**: 463-5.

Trainor, F.R. & Shubert, L.E. (1974). *Scenedesmus* morphogenesis. Colony control in dilute media. *Journal of Phycology* **10**: 28-30.

Trifonova, I.S. (1988). Oligotrophic-eutrophic succession of lake phytoplankton. In: F.E.Round (1988).

- Tunney, H., Carton, O.T., Brookes, P.C. & Johnston, E.E. (eds) (1997). *Phosphorus loss from soil to water*. CAB International , Wallingford.
- Turner, J.T., Tester, P.A. & Ferguson, R.L. (1988). The marine Cladoceran *Penilia avirostris* and the "microbial loop" of pelagic food webs. *Limnology & Oceanography* **33**(2): 245-255.
- UNESCO (1971). Convention on Wetlands of International Importance especially as Waterfowl Habitat. Ramsar, Iran.
- Urabe, J., Nakanishi, M. & Kawabata, K. (1995). Contribution of metazoan plankton to the cycling of nitrogen and phosphorus in Lake Biwa. *Limnology & Oceanography* **40**: 232-241.
- Utkilen, H.C., Oliver, L.R. & Walsby, A.E. (1985). Buoyancy regulation in a red *Oscillatoria* unable to collapse gas vacuoles by turgor pressure. *Archiv für Hydrobiologie* **102**: 319-329.
- Vadstein, O., Brekke, O., Andersen, T. & Olsen, Y. (1995). Estimation of phosphorus release rates from natural zooplankton communities feeding on planktonic algae and bacteria. *Limnology & Oceanography* **40**: 250-262.
- Van Liere, L., Mur, L.R., Gibson, C.E. & Herdman, M. (1979). Growth and physiology of *Oscillatoria agardhii* and some related species, a survey. *Developments in Hydrobiology* **2**: 67-77.
- Van Liere, L. & Walsby, A.E. (1982). Interactions of cyanobacteria with light. In: N.G.Carr & B.A.Whitton (eds.) *The Biology of the Cyanobacteria*. Blackwell, Oxford.
- Vincent, C., T.Davies, T. & Beresford, A. (1979). Recent changes in the level of Lake Naivasha, Kenya, as an indicator of equatorial westerlies over East Africa. *Climate Change* **2**: 175-189.
- Viner, A.B. & Smith, I.R. (1973). Geographical, historical and physical aspects of Lake George. *Proceedings of the Royal Society of London B*. **184**: 235-270.
- Vollenweider, R.A. (1974). *A Manual on Methods for Measuring Primary Production in Aquatic Environments 2nd edition*. IBP Handbook No. 12, Blackwell, Oxford.

Webster, I.T. & Hutchinson, P.A. (1994). The effect of wind on the distribution of phytoplankton cells in lakes revisited. *Limnology & Oceanography* **39**(2): 365-373.

Weisse, T. (1989). The microbial loop in the Red Sea: dynamics of pelagic bacteria and heterotrophic nanoflagellates. *Marine Ecology Progress Series* **55**: 241-250.

D.Werner, ed. (1977). *The ecology of diatoms*. Blackwell, Oxford.

Wetzel, R.G. & Likens, G.E. (1991). *Limnological Analyses, 2nd edition*. Springer-Verlag, New York.

Woodruff, S.L., House, W.A., Callow, M.E. & Leadbeater, B.S.C. (1999). The effects of biofilms on chemical processes in surficial sediments. *Freshwater Biology* **41**: 73-89.

Wright, D., O'Brien, W.J. & Vinyard, G.L. (1980). Adaptive Value of Vertical Migration: A Simulation Model Argument for the Predation Hypothesis. In: Kerfoot (1980).

Youdeowei, A., Ezedinma, F.O. & Onazi, O.C. (eds) (1986). *Introduction to Tropical Agriculture*. Longman, Harlow.

Guides to algal identification

Barber, H.G. & Haworth, E.Y. (1981). *A guide to the morphology of the Diatom Frustule*. Freshwater Biological Association, Ambleside.

Bellinger, E.G. (1974). A Key to the identification of the more common Algae found in British freshwaters. *Water Treatment & Examination* **23**(1): 76-131.

Bourrelly, P. (1981). *Les Algues d'eau douce: algues jaunes et brunes*. N. Boubée, Paris.

Bourrelly, P. (1985). *Les Algues d'eau douce: algues bleues et rouges*. N. Boubée, Paris.

Bourrelly, P. (1990). *Les Algues d'eau douce: algues vertes*. N. Boubée, Paris.

Krammer, K. & Lange-Bertalot, H. (1997). *Süßwasserflora von Mitteleuropa: Bacillariophyceae 1. Teil: Naviculaceae*. Gustav Fischer, Jena.

Lind, E.M. & Brook, A.J. (1980). *Desmids of the English Lake District*. Freshwater Biological Association, Ambleside.

General references

Chapman, V.J. & Chapman, D.J. (1973). *The Algae, 2nd edition*. Macmillan, London.

Cooke, G.D., Welch, E.B., Peterson, S.A. & Newroth, P.R. (1993). *Restoration and Management of Lakes and Reservoirs*. Lewis, Boca Raton.

Donia, N.S. (1998). *Integration of GIS and Computer Modelling to Study the Water Quality of Lake Naivasha, Central Rift Valley, Kenya*. MSc thesis, ITC, Netherlands.

Edmondson, W.T. & Winberg, G.G. (1971). *A Manual on Methods for the Assessment of Secondary Productivity in Fresh Waters* IBP Handbook No. 17, Blackwell, Oxford.

Fay, P. (1983). *The Blue-greens*. Edward Arnold, Baltimore.

Harris, G.P. (1986). *Phytoplankton Ecology. Structure, Function and Fluctuation*. Chapman & Hall, London.

Jones, J.G. (1979). *A guide to methods for estimating Microbial Numbers and Biomass in fresh water*. Freshwater Biological Association, Ambleside.

Morgan, N.E. (1998). *Groundwater chemistry and Quality assessment of the Lake Naivasha area, Kenya*. MSc thesis, ITC, Netherlands.

Pacini, N. (1994). *Coupling of land and water: Phosphorus Fluxes, Tana River, Kenya*. PhD Thesis, University of Leicester.

Podder, A.H. (1998). *Estimation of long-term inflow into Lake Naivasha from the Malewa Catchment, Kenya*. MSc thesis, ITC, Netherlands.

Strickland, J.D. & Parsons, T.R. (1968). *A Practical Handbook of Seawater Analysis*. Fisheries Research Board of Canada.