Effect of eutrophication on phytoplankton in the Mwanza Gulf (Lake Victoria, Tanzania)

A mesocosm and modelling study

M.Sc. Thesis by Christian Hazenoot

February 2012

Aquatic Ecology and Water Quality Management Group

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Abstract

Nutrient enrichment experiments were conducted near the Mwanza Gulf of Lake Victoria in Tanzania in the short rainy season to study the effects of the predicted increase of eutrophication processes in the future. Furthermore, a mini-model was developed to study the phytoplankton response in one of the experiments. This model was also applied to the Mwanza Gulf to determine if phytoplankton growth is likely to be limited by light or another factor. The mesocosm experiments and the mini-model demonstrated that, when light is sufficient, phytoplankton grows until nutrients become deficient. Cyanobacteria did not show the expected increase with higher nutrients loads or low N:P ratios, indicating that cyanobacterial dominance is not solely related to high nutrients or low N:P ratios. Furthermore, varying N:P ratios of the nutrients loads resulted in N-limited growth at a ratio of 10:1. Comparison to current nutrient concentrations in the Mwanza Gulf indicates that the phytoplankton in the Mwanza Gulf is probably not severely limited by N, rather moderately.

In addition, the mini-model was used to study whether or not the phytoplankton in the Mwanza Gulf was limited by light or nutrients. The measured field values showed large differences in the mixing depth and chlorophyll levels of the phytoplankton in the Mwanza Gulf. Consequently, the model results indicated a large variation in the probability of light limited phytoplankton growth. This indicates that another factor is probably limiting phytoplankton growth to the greatest extent, very probably not N or P because measured nutrient concentrations in the Mwanza Gulf do not give an indication that limiting effects would be expected. Probably the factor that limits phytoplankton to the greatest extent in the Mwanza Gulf is the high background attenuation caused by high suspended organic and inorganic matter. Because light limits phytoplankton growth, via high background attenuation, it is not likely that increased eutrophication processes, which increase nutrient concentrations, will lead to higher phytoplankton production.

1. Introduction

Lake Victoria is Africa´s largest freshwater lake and the second largest in the world, covering 68.800 square kilometers with a mean depth of 40 meters. The lake is located in three different countries: Kenya (6% of the area), Tanzania (51%) and Uganda (43%). Its catchment area consists of almost 200.000 km^2. The lake supports the largest freshwater fisheries in the world, approximately 1.000.000 tons of fish products are caught each year (Kolding et al. 2008).

In the last decades the human population around Lake Victoria has increased considerably (Figure 1.1). The population has grown from 4.6 million in 1932 to 27.7 in 1995 (Verschuren et al. 2002) and was estimated at 38 million in 2010. This growth leads to increases in domestic and industrial waste- and sewage water, firewood burning and agricultural land use (Odada et al. 2004). Soil erosion and runoff are the consequences of the growing demand for agricultural land use, leading to increased nutrient input into the lake (Odada et al. 2004). Atmospheric deposition and land runoff are responsible for approximately 90% and 94% of the phosphorous and nitrogen input into the lake (Scheren et al. 2000).

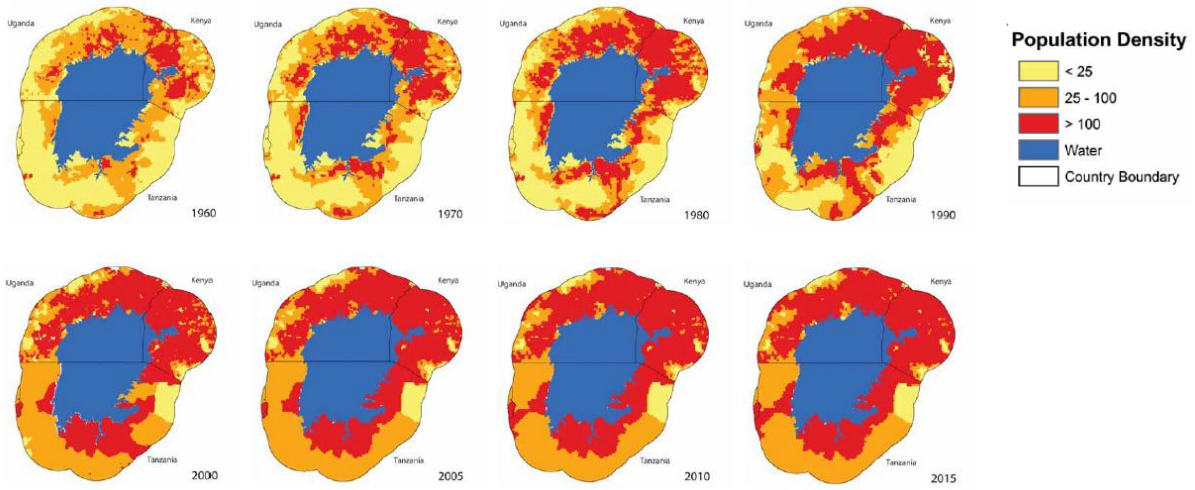

Figure 1.1 **Development in the population density around Lake Victoria between 1960-2010, prediction for 2015 is also included.**

For these reasons the growth of the human population has led to eutrophication of the lake. Eutrophication is the process of an ecosystem becoming more productive by nutrient enrichment stimulating primary producers (Dodds 2002). Nutrient enrichment of Lake Victoria is clearly visible in the phosphorus concentration of the lake, since the 1960s the total phosphorous concentration has more than doubled (Mugidde 2001, Hecky et al. 2010). This correlates to increased chlorophyll concentrations; chlorophyll levels offshore increased by a factor three (Talling 1965, Hecky 1993) and inshore this was near factor five (Talling 1965, Mugidde 2001).

The consequences of eutrophication are visible in several aspects*;* the water hyacinth nuisance in the 1990`s (Albright et al. 2004), higher chlorophyll densities, changes in phytoplankton composition (Kling et al. 2001) and increased anoxic conditions (Hecky 1994).

The phytoplankton composition changed due to the eutrophication. The growth and biomass of diatoms increased, which depleted the silica (Si) content of the lake (Hecky 1993, Kling et al. 2001, Verschuren et al. 2002). Consequently the abundance of diatoms decreased significantly, because Si is necessary for their cell walls. This resulted in a shift in dominance from diatoms to N-fixing cyanobacteria, nowadays they dominate the algal community the entire year (Kling et al. 2001). Several species of cyanobacteria contain gas vesicles that allow them to regulate their buoyancy and therefore also to form scums on the water surface, which may lead to deoxygenating of the water column when large parts of the scum dies off. Because of this, and in combination with the fact that some species of cyanobacteria can produce toxins which can be life-threatening for animals and humans (Pouria et al. 1998), a proliferation of cyanobacteria can lead to nuisance, oxygen deficit in the water column and health threats. Cyanobacteria are also a poor food-source for zooplankton, due to their large colony size and potential toxin content (Ghadouani et al. 2003).

Moreover, Lake Victoria became more deoxygenated due to eutrophication, with as a consequence a reduction of suitable habitat for fish and even fish kills (Ochumba 1990). The increased primary production caused by eutrophication has increased oxygen concentrations in the upper water layer (epilimnion), which strengthens thermal stratification. Thermal stratification occurs when the upper water layers are heated more rapidly than that the heat is distributed by mixing. Due to these temperature, and consequently density differences, the water layers are not easily mixed. The oxygen concentration in the lower water layers (hypolimnion) decreased due to increased breakdown of organic matter and because of the

more persistent thermal stratification, which hampers oxygen exchange through water layers (Hecky 1994). The deoxygenation of the hypolimnion also raised the denitrification rates, reducing nitrogen availability (Hecky 1993). This results in low nitrogen (N) to phosphorus (P) ratios in the lake and possible N-limitation, which likely promotes N-fixing cyanobacteria (Kling et al. 2001).

In addition to the ecosystem change due to eutrophication, the introduction of the Nile perch (*lates Niloticus*) has caused a destructive change. Nile perch, which was introduced between 1954 and the early 1960`s in an attempt to increase fishery productivity (Pringle 2005), led to the extinction or near extinction of hundreds haplochromines species (Witte et al. 1992, Witte et al. 2007), which previously accounted for approximately 80 percent of the fish stocks (Kudhongania 1974). The Nile perch boom greatly simplified the food web, from a diverse population of endemic fish species to a food web dominated by only three different fish species and a shrimp, namely: Nile perch, Nile Tilapia (Oreochromis niloticus), *Rastrineobola argentea* (also known as dagaa), and the freshwater shrimp Caridina nilotica (Witte et al. 1992).

The fishing industry however, benefitted greatly. The amount of fishermen and fishing vessels increased between the 1970`s and 2004 with a factor five and six respectively (Kolding et al. 2008). Nowadays approximately 10 million people make their livelihood in the fisheries sector (Johnson 2010). This fishing intensity has led to concerns of overfishing and calls to decrease fishing intensity, because increasing intensity would lead to decline of the stocks (Balirwa et al. 2003, Cowx et al. 2003, Matsuishi et al. 2006).

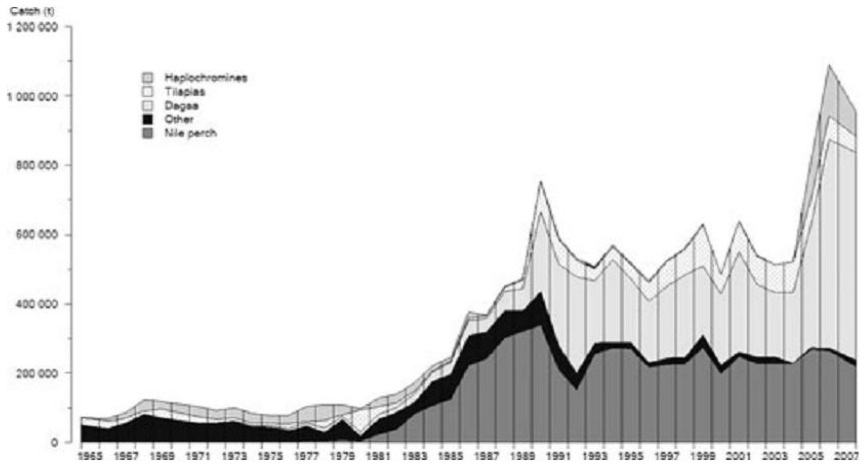

Figure 1.2 **Total fish catch of major species and groups of species in lake Victoria between 1965-2007. Data from Kolding et al. (2008). The figure is adopted from Hecky (2010).**

In contrast, Kolding et al. (2008) state that there is no proof that the Nile perch stocks are declining or that there are signs of overexploitation (see Figure 1.2). Their hypothesis is that the eutrophication of Lake Victoria, resulting in increased productivity, has led to the increase of fish stocks. Therefore the key factor in explaining the state of Lake Victoria is eutrophication and not fishing pressure. If eutrophication continues, it may lead to lower primary productivity due to self-shading of algae and lower transparency of the water. There are already signs that phytoplankton is light-limited (Silsbe et al. 2006), therefore increasing eutrophication will not lead to higher productivity and fish biomass. Also, eutrophication promotes the growth of less edible cyanobacteria. Continuing eutrophication could lead to increased anoxic conditions as well, with the consequence that there is less suitable habitat for fish.

The objective of this study is to test the effects of eutrophication on the phytoplankton abundance and composition. This is done by setting up mesocosms experiments.

The increased nutrient availability, that is mimicked in the experiments, are hypothesized to result in one of these four conditions:

1. Eutrophication might lead to increased phytoplankton biomass and cyanobacterial dominance through increased amounts of nutrients.
2. When P is limited, eutrophication will probably lead to decreased phytoplankton biomass and decreased cyanobacterial dominance.
3. When N is limited, eutrophication will probably not lead to increased phytoplankton biomass, it could even decrease, but cyanobacterial dominance will probably increase.
4. Eutrophication will probably not lead to higher phytoplankton biomass when light is limited, but cyanobacterial dominance will probably increase.

In this study the effect of eutrophication on the phytoplankton biomass and composition is tested with three experiments, evaluating 1) the effects of increasing nutrient load, 2) the effects of different N:P ratios and 3) the effects of the combination of nutrients and light respectively. It is expected that increased nutrient load will lead to higher phytoplankton biomass and increased dominance of cyanobacteria. Furthermore, it is expected for the N:P ratio experiment that phytoplankton will grow until N becomes limited and that cyanobacterial dominance increases with low N:P ratios. For the experiment with the different amounts of light and nutrients it is expected that chlorophyll levels increases with higher light and nutrient concentrations. It is hypothesized that the phytoplankton respond differently to the different

light and nutrient conditions, to more shade tolerant algae at low light conditions and more cyanobacteria at high nutrient conditions. With a mini-model the light experiment is analyzed more in-depth, to evaluate whether the different treatments of the last experiment are light or nutrient limited. Moreover, the mini-model is used to determine if the Mwanza Gulf is more likely to be limited by light or nutrients.

2. Material & Methods

2.1 Experiments

In 2010 three different mesocosms experiments were conducted near the Mwanza Gulf of Lake Victoria (Tanzania, Figure 2.1) during the short rainy season in September-October 2010, which is characterized by cyanobacterial dominance. Maize storage buckets with a capacity of circa 40 L were used as mesocosms and incubated with water prior to the experiment to prevent an effect of plasticizers on phytoplankton growth. Water from Lake Victoria was filtered with a 75 µ mesh-size zooplankton net to exclude zooplankton and pumped in the cosms. The nutrient concentration of the lake water was approximately 0.08 mg P/L^{-1}, 0.83 mg N/L^{-1} and the molar N:P ratio was 23:1 at the time of the experiments. The mesocosms were covered with untreated mosquito net, to prevent external influences like leaves falling in or an invasion of mosquito larvae. Three different experiments were conducted:

1. **Nutrients experiment**. The aim of this experiment was to determine the effects of different nutrient concentrations on phytoplankton abundance and composition. Nutrients were added in one single addition with molar N:P ratios of 15:1. There were four different treatments: i) Control treatment with no nutrient additions, ii) Low treatment with 0.05 mg P/L^{-1}, iii) Medium treatment with 0.35 mg P/L^{-1} and iv) High treatment with 0.75 mg P/L^{-1} nutrients added (see Table 2.1). The experiment lasted 12 days and every treatment had 8 replicates.

2. **N:P ratio experiment**. The aim of this experiment was to determine the effect of modified N:P ratios on phytoplankton abundance and composition. Nutrients were added in one single addition. The N:P ratio was modified in the different treatments by changing the nitrogen additions, while the phosphorus additions (0.05 mg P/L^{-1}) stayed the same. The control treatment did not receive nutrients. There were four different treatments: i) Control treatment with only lake water and thus no nutrient additions and no change of the N:P ratio, ii) Low treatment with a N:P ratio of 5:1, iii) Medium treatment with a N:P ratio of 10:1 and iv) High treatment with a N:P ratio of 20:1 (see Table 2.1). The experiment lasted for 13 days and every treatment had 8 replicates.

3. **Light & Nutrients experiment.** The aim of this experiment was to determine the effects of different light and nutrients regimes on the phytoplankton abundance and composition. Nutrients were added in one single addition with molar N:P ratios of 15:1. The different light regimes were made by covering the cosms with several layers of untreated mosquito nets. There were 7 different treatments: i) Control with natural light and no nutrients additions, ii) Low light & Low nutrients (LL) with 10% of natural light and a nutrient addition of 0.05 mg P/L^{-1}, iii) Low light & High nutrients (LH) with 10% of natural light and a nutrient addition of 0.75 mg P/L^{-1}, iv) Medium light & Low nutrients (ML) with 50% of natural light and addition of 0.05 mg P/L^{-1}, v) Medium light & High nutrients (MH) with 50% of natural light and addition of 0.05 mg P/L^{-1}, vi) High light & Low nutrients (HL) with natural light and addition of 0.75 mg P/L^{-1} and vii) High light and High nutrients treatment (HH) with natural light and addition of 0.75 mg P/L^{-1} (see Table 2.1). The experiment lasted for 11 days and every treatment had 5 replicates.

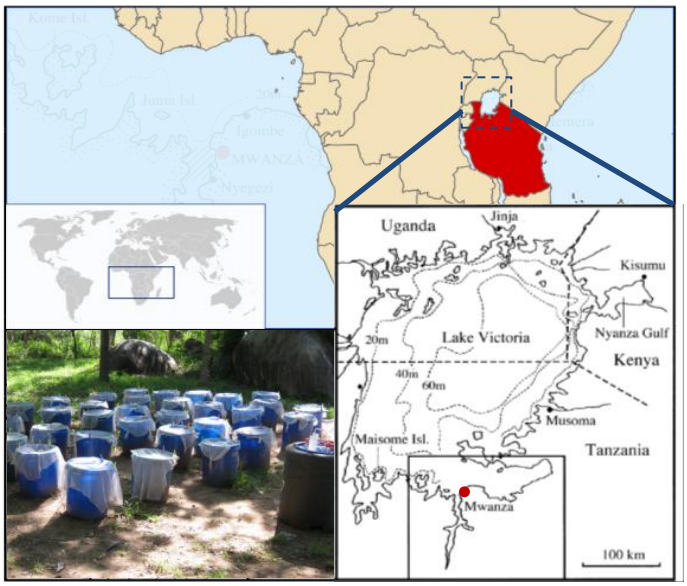

Figure 2.1 **Lake Victoria and the location of the experiment indicated by the red dot. In the lower left corner a picture is displayed of the setup of the experiments. Map is adopted and changed from Witte et al. (2007).**

Sampling took place on days 1, 5, 7 and 11 of the Nutrient experiment, on days 1, 7 and 11 (N:P ratio experiment) and on days 1, 5, 9 and 11 of the Light and Nutrient experiment.

Phytoplankton samples (4,5ml) were taken for determination of phytoplankton groups by pulse-amplitude modulated fluorometry (Phyto-PAM). Samples were preserved with 20 µl 25% glutaraldehyde and stored in the fridge at -4˚C, before they were analyzed. The Phyto-PAM analyses were done at NIOO (The Netherlands Institute of Ecology) Nieuwersluis (the Netherlands) with a Phyto-PAM (Walz). Chlorophyll (Chl) and oxygen were at least measured once, but usually twice a day with a Hydrolab DS5 Multiprobe (Hack Company) equipped with conductance, temperature, pH, depth and chlorophyll *a* sensors. Water was homogenized before sampling and measuring.

After the analyses, remarkable and inexplicable differences were obtained between the measurements of the Phyto-PAM and the chlorophyll measurements by the Hydrolab DS5 Multiprobe; the chlorophyll levels differed a factor 2-5. Because these levels could not logically be explained, the effect of the preservation by glutaraldehyde was tested. A water sample was taken in Wageningen (the Netherlands) and enriched with cyanobacteria to obtain a sample with equal abundance of the three phytoplankton groups. This sample was analyzed in different batches, with and without glutaraldehyde addition. The glutaraldehyde addition had the same concentration and volume as the samples that were taken in Tanzania. Three batches were stored in the fridge at -4˚C for one, two or three weeks. The results of these tests are presented in Figure 2.2. These results show that preservation with glutaraldehyde degrades the phytoplankton. Diatoms are very sensitive, after a short period they are not detectable anymore, while green algae increased strongly. Only cyanobacteria abundance was constant. Therefore only the data of cyanobacteria abundance are presented, the data of diatoms and green algae are left out.

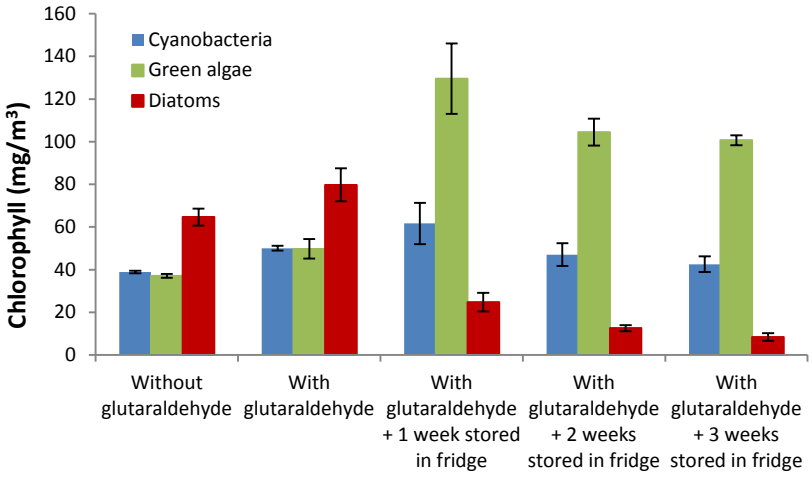

Figure 2.2 **Effect of glutaraldehyde on the three phytoplankton groups as measured by the Phyto-PAM.**

Table 2.1 **Nutrient additions for the different treatments of the three experiments and averaged values of current nutrient concentrations (2009-2011) in the Mwanza Gulf. When the molar N:P ratio is not specifically noted it is 15:1, and when the amount of light is not explicitly stated it is natural light. Symbols of Light & Nutrients treatment stand for: C=Control, LL=Low light & Low nutrients, LH=Low light & High nutrients, ML=Medium light & Low nutrients, MH=Medium light & High nutrients, HL=High light & Low nutrients, HH=High light & High nutrients. Data of nutrient concentrations in the Mwanza Gulf from Cornelissen (unpublished data).**

Nutrients			(molar) N:P ratio				Light & Nutrients				Lake		
	mg/L^{-1} P	mg/L^{-1} N		mg/L^{-1} P	mg/L^{-1} N	Molar N:P ratio		mg/L^{-1} P	mg/L^{-1} N	Light (%)	mg/L^{-1} P	mg/L^{-1} N	Molar N:P ratio
Control	0.00	0.00	Control	0.00	0.00		C	0.00	0.00	±100	0.08	0.87	23.28
Low	0.05	0.34	Low	0.05	0.11	5:1	LL	0.05	0.34	±10			
Medium	0.35	2.73	Medium	0.05	0.23	10:1	LH	0.75	5.09	±10			
High	0.75	5.09	High	0.05	0.45	20:1	ML	0.05	0.34	±50			
							MH	0.75	5.09	±50			
							HL	0.05	0.34	±100			
							HH	0.75	5.09	±100			

2.2 Statistical analyses

The experiments were analyzed with repeated measures ANOVA, because multiple measurements were taken during the experiments to monitor development of phytoplankton. For the Nutrients and N:P ratio experiments there was one 'between' factor (treatment) and one 'within' factor (time). Both experiments had four different treatments with eight replicates each. The Light & Nutrients experiment had a slightly different design with two 'between' factors (light and nutrient treatment), and one 'within' factor (time). To obtain more statistical power the control treatment was left out, because without the control treatment the experiment satisfies the conditions of a factorial design. To attain a normal distribution, data of the three different experiments were logarithmic transformed and the residuals were tested with a Shapiro-Wilk test. Because there were still some deviations from normality, rank transformation was also performed. In all the cases the results of the rank transformation was in the same order as the logarithmic transformed data, the F-values differed only slightly between the logarithmic and rank transformed data. The differences were so small that the results of the test, significant or not, were different for the different transformations. This result shows that repeated measures ANOVA is robust to violation of normality (Sokal and Rohlf 1995). Only the results of the statistical analyses with logarithmic transformed data are displayed. Missing values in the N:P ratio experiment were replaced with a closest match method. The average value of four cosms with the closest scores on chlorophyll at adjacent time points was substituted for the missing value (Elliott and Hawthorne 2005). For the N:P ratio experiment the last three samples were left out in the analyses, because those samples contained missing values and the chlorophyll levels had decreased to low values because nutrients were exhausted. Those decreased chlorophyll levels are not interesting, since they do not give any information about the effect of different amounts of nutrients on the phytoplankton biomass. When data did not meet the compound symmetry assumption, a Greenhouse-Geisser correction was applied on the degrees of freedom. Post-hoc tests on treatments, the 'between' factor(s), were performed with a Tukey test, or if the assumption of homogeneity of variances was violated with a Dunnett T3 test. However it was not possible to perform a Dunnett T3 test on the repeated measures analyses of the Light & Nutrients experiment when the data had heterogeneous variances, because there were two 'between' factors. Although ANOVA is robust to violations of this assumption (Glass et al. 1972), the conservative Bonferroni post-hoc test is used in these situations. The statistical analyses were performed with SPSS 19 for Windows.

2.3 Model description

2.3.1 Experiment

A model was made to describe the effects of the different light and nutrient treatments of the Light & Nutrients experiment on phytoplankton. The model was based on the phytoplankton models of Huisman and Weissing (1999). These models describe light limitation over the water column. The combination of light and nutrient limitation was described with the Liebig law, taking the minimum of both limitation functions. It was assumed that phytoplankton is equally distributed over the water column, and that there is no niche differentiation among species using different parts of the underwater light spectrum (Stomp et al. 2007). Furthermore it was assumed that there is no photoadaptation; the cellular or ecological response of phytoplankton to changes in light intensity.

Photoinhibition was included in the model, because Lake Victoria is located close to the equator and receives high levels of solar irradiance. Photoinhibition is the reduction of the photosynthetic rate due to high light, which is caused by damage of the photosynthetic systems of cells. The model of Huisman and Weissing (1999) was extended with the incorporation of photoinhibition as described by Gerla et al. (1995). The phytoplankton (A) growth at a certain position in the water colomn (z) is described by the following differential equation, in which phytoplankton biomass is expressed as chlorophyll in mg/m^3 (see for parameter values and units Table 2.2):

$$\frac{dA}{dt} = P_{max}A \cdot \min \left(\frac{I_z}{\frac{I_k}{I_{opt}^2} I_z^2 + \left(1 - 2\frac{I_k}{I_{opt}}\right) I_z + I_k}, \frac{Nu}{Nu + k} \right) - lA \qquad \textbf{[1]}$$

In which P_{max} is the maximum phytoplankton growth rate. Phytoplankton growth depends on light (I_z), nutrients (Nu), which are described with two monod equations, and a loss factor (l). The parameters I_k and I_{opt} are the onset of light limited phytoplankton growth and the optimal light intensity for phytoplankton growth, respectively. The parameter *k* is the half saturation constant of nutrient limitation for phytoplankton growth.

The amount of light I_z available at a certain water depth (z) in the water column for phytoplankton growth depends on self-shading of algae (k_a) and background extinction (k_b). Light intensity I_z is calculated with the law of Lambert-Beer:

$$I_z = I_{in} e^{-k_b \cdot z - k_a \cdot z} \quad \textbf{[2]}$$

In which I_{in} is the amount of light just below the water surface. The parameters k_b & k_a where obtained from field data (Cornelissen, unpublished data).

The resulting light-limitation is obtained by integrating the following Monod equation over the water column:

$$Light\ limitation = \frac{1}{d} \int_0^d \frac{I_z}{\frac{I_k}{I_{opt}^2} I_z^2 + \left(1 - 2\frac{I_k}{I_{opt}}\right) I_z + I_k} \, dz \quad \textbf{[4]}$$

This function can be solved analytically.

Daily fluctuations in incoming radiation I_{in} is calculated with a sinus-function, where I_{max} is calculated from field data of the Mwanza Gulf (Cornelissen, unpublished data). The sinus-function, mimicking daily fluctuations in radiation, is positive during daytime and negative at nights. As negative light intensity is obviously not possible; these values were set to zero with a max function in the equation:

$$I_{in} = max(I_{max} \sin\ 2\pi t - \pi\ , 0) \quad \text{(with t=time in days)} \quad \textbf{[3]}$$

The available nutrients (Nu) for phytoplankton growth are described by another differential equation. The phytoplankton uses a specific amount of nutrients per chlorophyll (*g*) and because there is no continuous nutrient loading in the experiment, the nutrient concentration can only decrease:

$$\frac{dN}{dt} = -gP_{max}A \cdot \min \left(\frac{1}{d} \int_0^d \frac{I_z}{\frac{I_k}{I_{opt}^2} I_z^2 + \left(1 - 2\frac{I_k}{I_{opt}}\right) I_z + I_k} \, dz \quad , \frac{Nu}{Nu+k} \right) \quad \textbf{[5]}$$

Nutrients are calculated in phosphorus concentrations, because it is assumed there is an excess of nitrogen due to the applied N:P ratio of 15:1. Nutrient input by decaying and lysis of dead phytoplankton was not included, because the effect is probably negligible due to the short duration of the experiment. The light treatments are calculated by a reduction (in percentage) of the incoming light intensity (I_{in}).

The parameters P_{max}, I_k and I_{opt} of the model were fitted to the chlorophyll *a* data of the Light and Nutrient experiment. The parameter P_{max} was fitted to the chlorophyll *a* data of the High light and High nutrient treatment (HH) with a value that was estimated from the growth data of the three experiments of this study, corrected for the loss factor. From the data of the Light & Nutrient experiment it became clear that phytoplankton was adapting to the nutrient conditions, the proportion of nitrogen and phosphorus in 1 mg Chlorophyll changed, or in other words: the phytoplankton changed its nutrient stoichiometry. The parameter g was varied to simulate the effects of different adaptations of phytoplankton to different nutrient conditions (see Table 2.2). From literature it is known that under high nutrient conditions phytoplankton can have a high uptake of phosphorus leading to an increasing biomass phosphorus ratio (Reynolds 2006). Phytoplankton can contain 8-16 times more phosphorus in its cells than their minimum requirement (Reynolds 2006).

The parameters of the light curve (I_K and I_{opt}, with $I_{opt} = 2 \cdot I_k$) were fitted to the low light treatments with a value that lies in the reported range of Mugidde (1993) for light intensity that defines the onset of light saturated photosynthesis (I_k), namely 128 - 240 µE m^{-2} s^{-1}.

2.3.2 Mwanza Gulf

The model was applied to the Mwanza Gulf as well, in order to evaluate which factor is most likely limiting phytoplankton growth. The above described mini-model was used, with the only exception that the nutrients concentration was set to a constant value (equation 5). Therefore this model was only depended on the availability of light and there was no feedback to nutrients. Consequently, the model outcomes are the maximum chlorophyll levels at a certain depth. When chlorophyll levels of measured field data were at this maximum level it was assumed that phytoplankton productivity is light limited and (more) limited by another factor when measured chlorophyll levels are lower than this maximum level. The field data, a total of 140 measurements, was measured in the Mwanza Gulf at 4 different sampling points, which were measured in triplicate between 2009-2011 in all the seasons. Measurements were done with a Hydrolab DS5 Multiprobe (Hack Company). The maximum water depth of these sampling points ranged from 4-10 meters. For every point the mixing depth was calculated as the depth at which the decrease of temperature over a depth interval was maximal. The average of the mixing depth for the three measurements per station per time was used. These mixing depths were used to calculate the average chlorophyll levels for the three measurements at every point, which were averaged to get the final chlorophyll level for every station per time. These average chlorophyll levels over mixing depth were taken for comparison with the model results. Data of average chlorophyll levels in the mixed water layer for the offshore sampling points (depth maximum 26 meter) were excluded, because (background) light attenuation was much lower for the offshore stations and assessment of the mixing depth became more inaccurate (see Figure 2.3, stations 5 and 6). The chlorohyll profiles were visually inspected on the occurrence of aggregation of chlorophyll at certain depths, reflecting phytoplankton that can regulate their buoyancy, but this was not occurring.

Water is assumed to be completely mixed over the entire mixed water layer, and this layer contributes equally to production. However, in the model the production in the mixed water layer is not equally, because resuspension mechanisms are not included. These mechanisms are not relevant for this study, because the total amount of available light for phytoplankton growth for the entire water column would be the same with or without resuspension mechanisms.

It is likely that the phytoplankton loss rate of the phytoplankton in the experiments is lower than the phytoplankton in the Mwanza Gulf, because phytoplankton losses due to grazing, flushing and sinking, were not present in the experiments. These losses were not present in the

experiments due to the experimental setup and because phytoplankton loss by sedimentation did not occur, for the cosms were homogenised twice a day to prevent sedimentation and to measure the chlorophyll content. These factors can contribute significantly to phytoplankton loss rate (Reynolds 2006). The loss factor was varied in order to (partly) correct for this, as well as for the above described situations in which mixing depth is deeper than euphotic depth (see Table 2.2 for parameter values).

Table 2.2 Parameter values of the model, and their units.

Parameter/State variable	Description	Unit	Default value	Source
Nu	Phosphorus concentration	g P m^{-3}	0.75[1]/0.05[2]/0.1[3]	Field observation
A	Phytoplankton biomass (Chlorophyll *a*)	mg Chl *a* m^{-3}		Field observation
P_{max}	Maximum growth rate per day	day^{-1}	2	Field observation
k	Half saturation of nutrient limitation	g P m^{-3}	0.005	Serizawa et al. (2011)
I_z	Light intensity at depth *z*	µE m^{-2} s^{-1}		Calculated by model
I_{in}	Light intensity at certain t just below water surface	µE m^{-2} s^{-1}		Calculated by model
I_k	Onset of light limitation	µE m^{-2} s^{-1}	135	Mugidde (1993)
I_{opt}	Optimal light for phytoplankton growth	µE m^{-2} s^{-1}	270	Mugidde (1993)
I_{max}	Maximum daily irradiance just below water surface	µE m^{-2} s^{-1}	950	Cornelissen, unpublished data
K_b	Background light attenuation	m^{-1}	0.6	Cornelissen unpublished data
k_a	Light attenuation phytoplankton	m^2 mg Chl a^{-1}	0.1	Cornelissen unpublished data
g	Phosphorus concentration of phytoplankton	g P/mg Chl *a*	0.004[1]/0.0006[2]	Arbitrary realistic value based on Reynolds (2010)
l	Phytoplankton loss rate	day^{-1}	0.15/0.20[3]/0.25[3]	Arbitrary value
d	Water depth	m^{-1}	0.5/4[4]	Field observation

[1]High nutrient treatments, [2] Low nutrient treatments, [3]Mwanza Gulf model, [4]varied for the Mwanza Gulf model

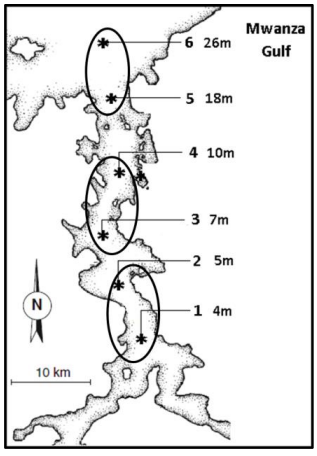

Figure 2.3 Location of the different sampling stations in the Mwanza Gulf.

3. Results

3.1 Nutrients experiment

The aim of the Nutrients experiment was to determine if increased nutrient loadings lead to increased chlorophyll biomass and whether there is an effect on the phytoplankton composition. The statistic results show significant differences between the chlorophyll levels of the different nutrient treatments ($p < 0.001$, Table 3.1 & Figure 3.1). The post hoc test revealed that there were significant differences between all the treatments (all $p < 0.001$, Table 3.1). The control treatment had the lowest levels of chlorophyll, followed by the low treatment, then the medium, and the chlorophyll levels were highest in the high nutrient treatment. There were significant effects of time ($p < 0.001$, Table 3.1) and time × nutrient treatment ($p< 0.001$, Table 3.1). The chlorophyll levels increased during the experiment (time) and the chlorophyll levels increased with more nutrients and time (time x treatment) (see Figure 3.1). At the end of the experiment the chlorophyll levels decreased, probably because the nutrients were depleted. However this was not the case for the control treatment; the chlorophyll level increased slightly after the start and did not drop at the end of the experiment (see Figure 3.1).

Table 3.1 **Results of repeated measures ANOVA for the Nutrients experiment.**

Model term	Entire time series[#]				
	d.f.	MS	F	Sig.	Post Hoc
Nutrient treatment	3	19.49	205.92	<0,001*	A,B,C,D
Error	28	0.09			
Time	20	12.10	282.10	<0.001*	
Time × Nutrient treatment	60	1.31	30.51	<0.001*	
Error	560	0.04			

* Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Dunnett T3 test are expressed in symbols, first symbols stands for Control treatment, second for Low, third for Medium, and fourth for High treatment

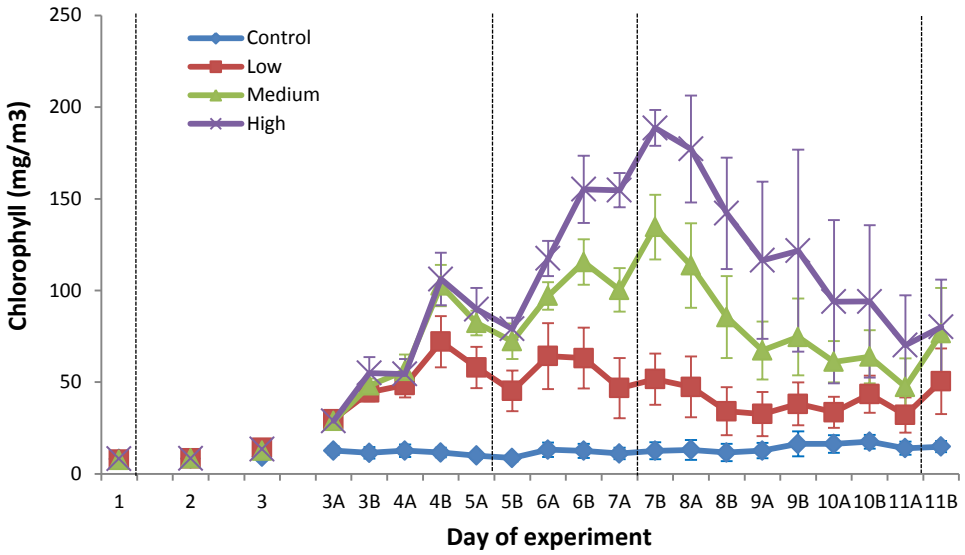

Figure 3.1 Chlorophyll levels (mg/m3) per measurement per nutrient treatment for the Nutrients experiment. For description of the different treatments and symbols see Table 2.1. A = morning measurement, B = afternoon measurement. The dotted lines mark the days at which samples for the measurements of cyanobacteria biomass were taken.

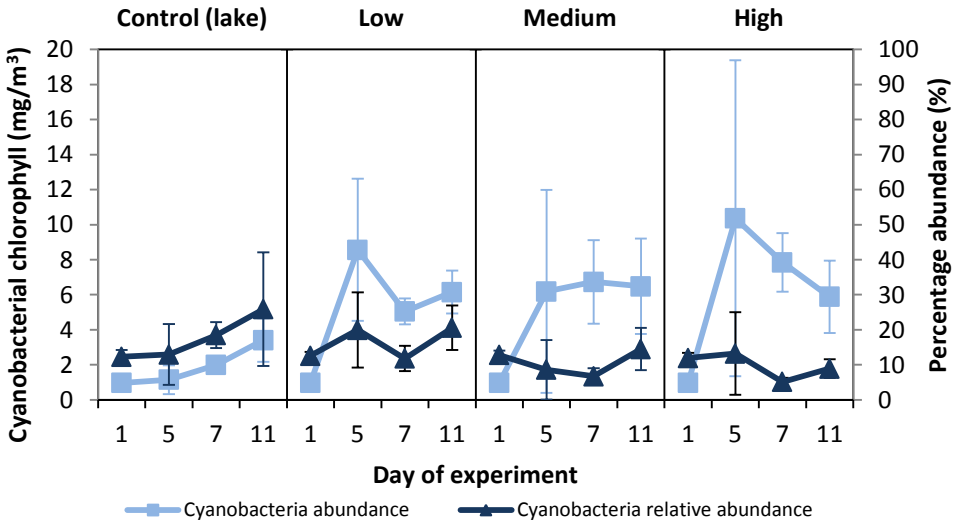

Figure 3.2 Absolute (in mg chlorophyll *a*/m^3) and relative (%) abundance of Cyanobacteria per treatment for the Nutrients experiment.

In Figure 3.2 the chlorophyll levels and percentage abundance of cyanobacteria per treatment are displayed. The chlorophyll levels were significantly different between the control and the other treatments ($p < 0.001$, Table 3.2). Between the three nutrient treatments there were no clear differences visible in the abundance of cyanobacteria. At the end of the experiment, day

11, the cyanobacteria chlorophyll levels were almost the same for the three nutrient treatments. However the chlorophyll levels for the low and medium treatments were much lower than for the high treatment. Thus the relative abundance of cyanobacteria decreased with more nutrients (see also Figure 3.2).

All four treatments started with similar abundance of cyanobacteria: 0.96 mg Chl/m^3 (SD 0.03).

Table 3.2 **Results of repeated measures ANOVA on cyanobacteria data for the Basic algae experiment.**

Model term	Cyanobacteria[#]				
	d.f.	MS	F	Sig.	Post Hoc
Nutrient treatment	3	3.20	13.40	<0.001	A,B,B,B
Error	28	0.24			
Time	3	23.47	29.06	<0.001*	
Time × Nutrient treatment	9	1.71	2.12	0.110*	
Error	84	0.92			

* Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Dunnett T3 test are expressed in symbols, first symbols stands for Control treatment, second for Low, third for Medium, and fourth for High treatment

3.2 N:P ratio experiment

In this experiment the effects of different N:P ratios on the phytoplankton composition and abundance was examined. There were significant effects of the different N:P ratio treatments on the chlorophyll levels ($p < 0.001$, Figure 3.3, Table 3.3), and the post hoc test indicated that there were significant differences between the i) control, ii) low and iii) medium & high N:P ratio treatments ($p < 0.001$, Table 3.3). The medium and high treatments differed clearly from the control and low treatments, since they had a higher biomass. However between these two (medium and high) treatments there was no significant difference in levels. The low treatment, with an N:P ratio of 5:1, clearly resulted in lower levels of chlorophyll than the medium and high treatment, showing that the Low treatment was nitrogen-limited. There were significant effects of time ($p < 0.001$, Table 3.3) and time × N:P ratio treatment ($p < 0.001$, Table 3.3), showing that the different N:P ratios had an (increasing) effect on chlorophyll levels. The chlorophyll of the control treatment, without nutrient addition, showed an increase from the start and no decline in levels at the end of the experiment.

At the end of the experiment, there was a strange distortion of the chlorophyll levels of the different treatments (see blue square Figure 3.3). The biomass level of the low treatment rose sharply, while the nutrients of this treatment should be exhausted at that moment. This pattern could not be logically explained and is therefore kept outside further analyses.

Table 3.3 Results of repeated measures ANOVA for the N:P ratio experiment.

Model term	Entire time series[#]				
	d.f.	MS	F	Sig.	Post Hoc
N:P ratio treatment	3	1.22	191.62	<0.001[*]	A,B,C,C
Error	28	0.01			
Time	14	1.60	489.90	<0.001[*]	
Time × N:P ratio treatment	42	0.05	15.46	<0.001[*]	
Error	392	<0.01			

[*] Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Dunnett T3 test are expressed in symbols, first symbols stands for Control treatment, second for Low, third for Medium, and fourth for High treatment

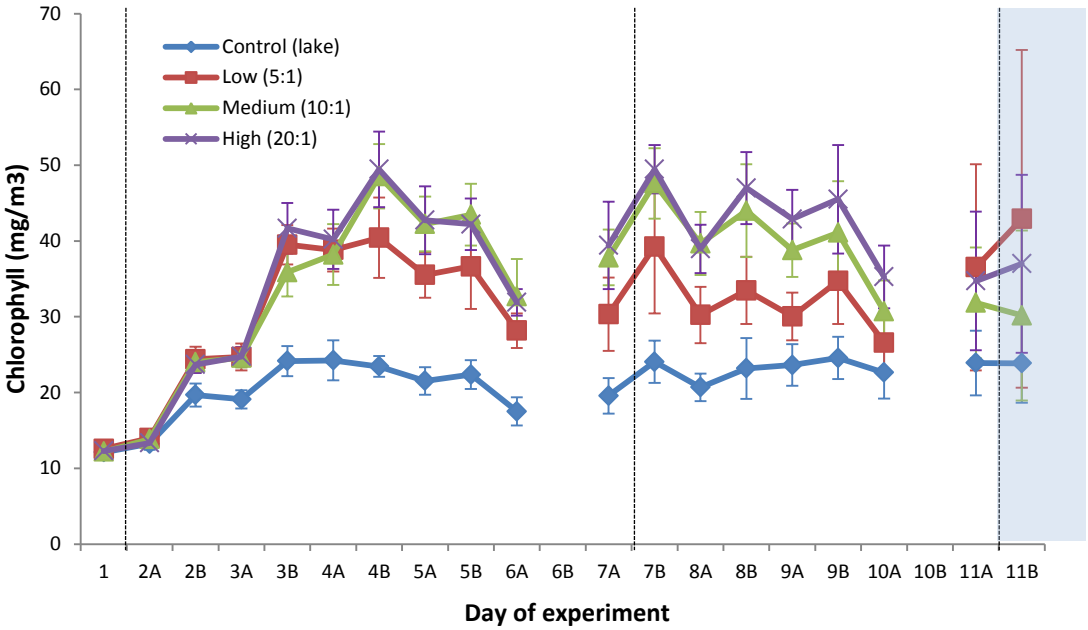

Figure 3.3 Chlorophyll levels (mg/m^3) per measurement per nutrient treatment for the N:P ratio experiment. For description of the different treatments and symbols see Table 2.1. A = morning measurement, B = afternoon measurement. The dotted lines mark the days at which samples for the measurements of cyanobacteria biomass were taken. The data within the blue square is not taken into account for the repeated measures ANOVA.

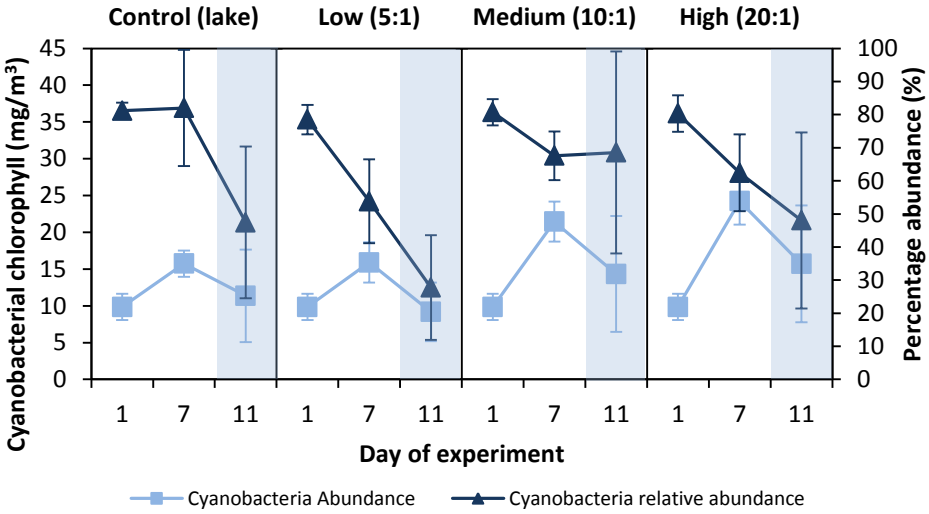

Figure 3.4 Absolute (in mg chlorophyll *a*/m^3) and relative (%) abundance of Cyanobacteria per treatment for the N:P ratio experiment. The data within the blue square is not taken into account for the repeated measures ANOVA.

The effect of the different N:P ratios on the abundance of cyanobacteria was also tested. The results seem to show a difference in abundance between the control & low treatment and the medium & high treatments, especially because the measurement of day 11 fell in the period where the chlorophyll levels showed a strange distortion. The statistical analysis, without the data of day 11 of the experiment, proved that there was a significant effect of the treatments on the absolute abundance of cyanobacteria ($p<0.001$, Table 3.4). The post hoc indicated that there were significant differences between the i) control &low treatment and ii) the medium and high treatment. Thus higher N:P ratios resulted in more cyanobacteria biomass. The relative abundance of cyanobacteria was also higher for the medium and high treatment compared to the low treatment, but less pronounced than the absolute abundance. The control treatment had the highest dominance of cyanobacteria during the experiment.

There was a significant time and time x N:P ratio treatment effect for cyanobacteria ($p < 0.001$ for both, Table 3.4), meaning that the chlorophyll levels increased through time and that the increase was different for the four treatments through time.

All four treatments started with similar abundance of cyanobacteria: 9.84 mg Chl/m^3 (SD 1.78).

Table 3.4 **Results of repeated measures ANOVA on cyanobacteria data for the N:P ratio experiment.**

Model term	Cyanobacteria[#]				
	d.f.	MS	F	Sig.	Post Hoc
N:P ratio treatment	3	0.17	17.85	<0.001	A,A,B,B
Error	28	0.10			
Time	1	5.85	612.39	<0.001	
Time × N:P ratio treatment	3	0.17	17.85	<0.001	
Error	28	0.10			

* Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Dunnett T3 test are expressed in symbols, first symbols stands for Control treatment, second for Low, third for Medium, and fourth for High treatment

3.3 Light & Nutrients experiment

The aim of the Light & Nutrients experiment was to determine the effects of different light and nutrient treatments on the abundance and composition of phytoplankton. The effects of the different treatments were clearly visible (Figure 3.5): chlorophyll was affected by nutrients and light and the control treatment was different from the other treatments (Figure 3.5). This is also visible in the statistical analyses; there was a significant effect of light ($p < 0.001$, Table 3.5) and nutrients ($p = 0.021$, Table 3.5). The post hoc test on the light treatments revealed that there were differences between i) Low light and ii) Medium and High light. Thus the chlorophyll levels increased with light and nutrients.

That light limitation occurred in this experiment is visible when looking at the chlorophyll levels within a nutrient regime, for example the High nutrient treatments. Within the High nutrient treatments the chlorophyll levels in the Low light treatment (LH) were much lower than in the High light treatment (HH), and the Medium light treatment (MH) had an intermediate chlorophyll level (Figure 3.5, for explanation of symbols see Table 2.1).

Nutrient limitation is visible; when comparing all the treatments there were interesting differences between the two Medium light treatments (ML & MH, see Figure 3.5). Until halfway the experiment they had approximately the same chlorophyll levels but afterwards the chlorophyll level of ML dropped to low values, pointing to nutrient limitation. It is likely that at that moment the nutrients were exhausted. Furthermore these treatments (ML & MH) were also light-limited, because the HL treatment had higher chlorophyll levels (until halfway the experiment) than the ML treatment, the same was the case for HH and MH (Figure 3.5). The drop in chlorophyll levels near the end of the experiment for all the treatments, except control, was probably caused by nutrient exhaustion. The control treatment showed no decline. From the beginning of the experiment the chlorophyll levels increased slightly while at the end of the experiment the levels did not decrease (see Figure 3.6).

Table 3.5 Results of repeated measures ANOVA for the Light & Nutrients experiment.

Model term	Entire time series[#]				
	d.f.	MS	F	Sig.	Post Hoc
Light treatment	2	4.29	33.71	<0.001	A,B,B
Nutrient treatment	1	0.78	6.09	0.021	
Light treatment × Nutrient treatment	2	0.46	3.59	0.043	
Error	24	0.13			
Time	19	7.85	223.27	<0.001	
Time × Light treatment	38	0.24	6.91	<0.001	
Time × Nutrient treatment	19	0.42	11.99	<0.001	
Time × Light treatment × Nutrient treatment	38	0.14	3.86	<0.001	
Error	456	0.04			

[*] Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Dunnett T3 test are expressed in symbols, first symbols stands for Control treatment, second for Low, third for Medium, and fourth for High treatment

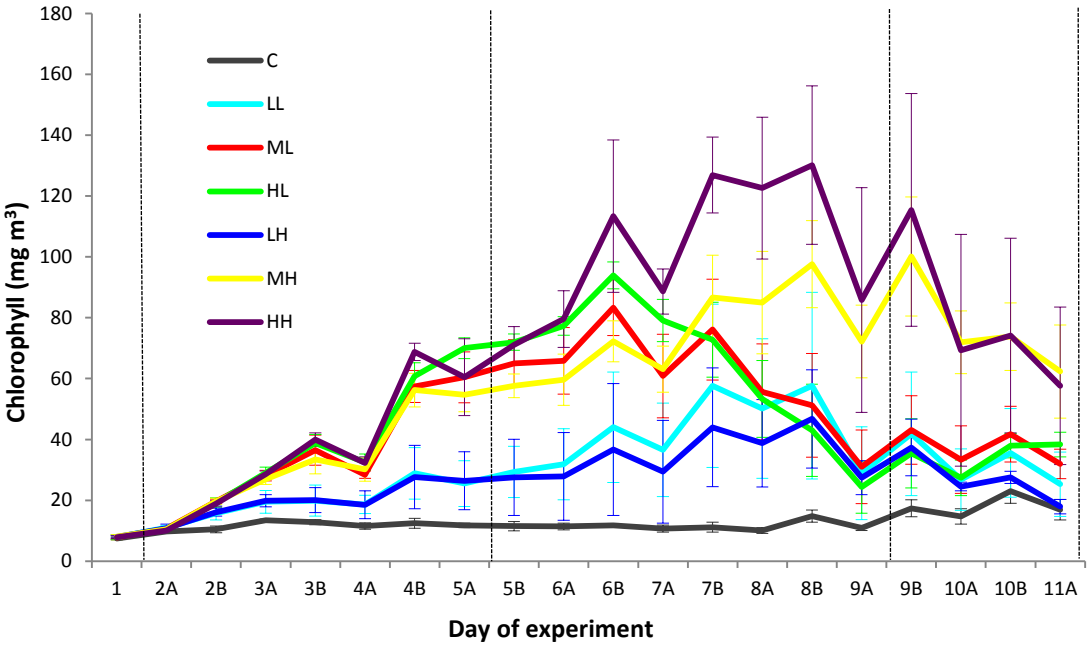

Figure 3.5 Chlorophyll levels (mg/m^3) per measurement per nutrient treatment for the Light & Nutrient experiment. Symbols of Light & Nutrients treatment stand for: C=Control, LL=Low light & Low nutrients, LH=Low light & High nutrients, ML=Medium light & Low nutrients, MH=Medium light & High nutrients, HL=High light & Low nutrients, HH=High light & High nutrients. A = morning measurement, B = afternoon measurement. The dotted lines mark the days at which samples for the measurements of cyanobacteria biomass are taken.

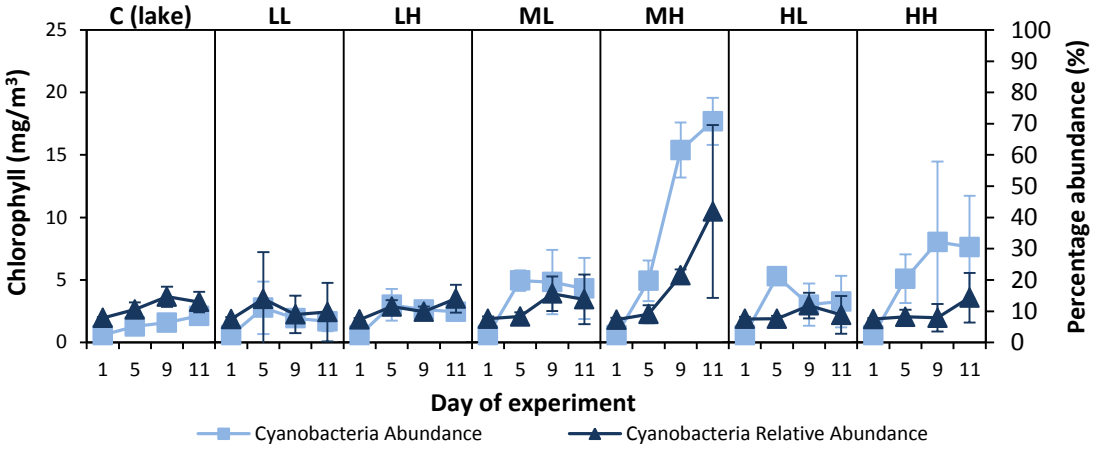

Figure 3.6 **Absolute (in mg chlorophyll *a*/m^3) and relative (%) abundance of Cyanobacteria per treatment for the Light & Nutrients experiment. For explanation of treatments and symbols see Table 2.1.**

Together with the influence of the different light and nutrient conditions on the chlorophyll levels, their effects on the abundance of cyanobacteria were studied. In all treatments the abundance of cyanobacteria increased from the start of the experiment (Figure 3.6). The MH and HH treatment had the highest abundance of cyanobacteria (Figure 3.6, light-blue line). The statistical analysis on the absolute abundance gave a significant effect of light and nutrients on cyanobacteria biomass ($p < 0.001$ for both cases, Table 3.6). this means that there is a significant difference in biomass of cyanobacteria between the two nutrient and the three light treatments. Cyanobacteria reached their highest biomass at high nutrients, and with light their biomass was highest at Medium light and lowest at Low light. In these statistical tests on the effects of light and nutrients all the treatments which received the same amount of light or nutrients were summed together, and in this way compared to the other light or nutrient treatments. However, the increase in cyanobacteria biomass with light and nutrients did not imply that they became more dominant, because the chlorophyll levels also increased. Only the MH treatment showed an increase in cyanobacteria dominance, but the standard deviation was very high.

All treatments started with similar abundance of cyanobacteria: 0.58 mg Chl/m^3 (SD 0.02).

Table 3.6 **Results of repeated measures ANOVA of cyanobacteria for the Light experiment, without the control treatment.**

Model term	Cyanobacteria[#]				
	d.f.	MS	F	Sig.	Post Hoc
Light treatment	2	4.57	21.97	<0.001	A,C,B
Nutrient treatment	1	3.82	18.34	<0.001	
Light treatment × Nutrient treatment	2	0.52	2.50	0.103	
Error	24	0.21			
Time	3	10.80	122.13	<0.001	
Time × Light treatment	6	0.82	9.22	<0.001	
Time × Nutrient treatment	3	1.28	14.43	<0.001	
Time × Light treatment × Nutrient treatment	6	0.24	2.74	0.019	
Error	72	0.09			

* Greenhouse-Geisser correction [#] Data logarithmic transformed
Post Hoc test results for the Bonferroni test are expressed in symbols, first symbols stands for the Low light treatment, second for Medium, third for the High light treatment

3.4 Model results

3.4.1 Experiment

The model predictions, with the adjustment of the phosphorous concentration of phytoplankton (*g*) to High or Low nutrient conditions, showed a reasonably good fit with the data of the Light and Nutrient experiment (Figure 3.7). The chlorophyll levels in the model showed the same dynamics as in the experiments: a steep increase until the nutrients were depleted and a strong decline afterwards. The increase in chlorophyll levels of the experiments was stronger than calculated by the model. Only the model's predictions of the two treatments with Low light were not completely in line with the data. For the LH treatment the model's prediction for the first 7 days were in line with the field measurements, afterwards the model did not follow the decline in chlorophyll, because in contrast to the experiment the nutrients were not exhausted in the model. For the LL treatment it was different; chlorophyll levels increased more slowly compared to the field data, but reached approximately the same level.

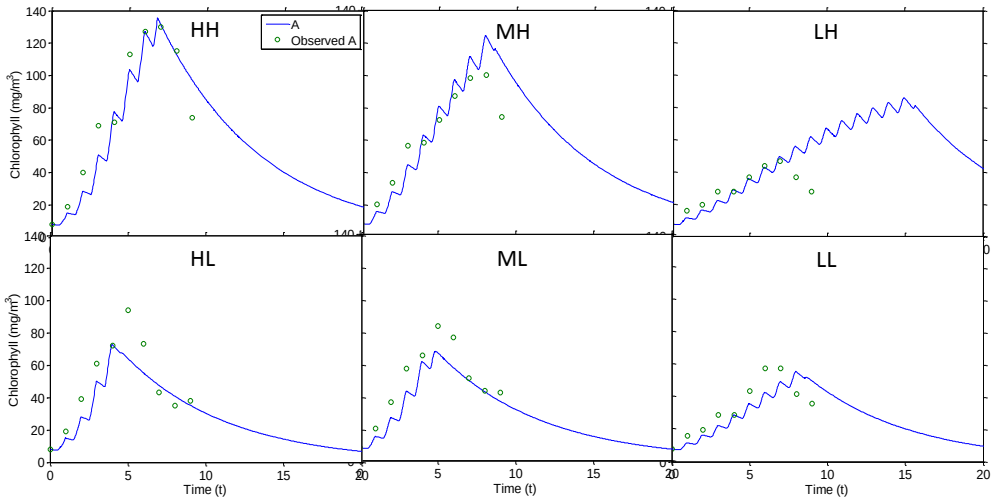

Figure 3.7 **Chlorophyll values as observed in the field (green) and predicted by the model (blue), for each treatment of the Light & Nutrient experiment. For description of the different treatments and symbols see Table 2.1.**

The model's predictions suggest that the decline of chlorophyll levels at the end of the experiment was due to nutrient exhaustion. Moreover, the results indicate that phytoplankton can change its nutrient uptake dynamics quite remarkably under different nutrient conditions. The difference in *measured* chlorophyll levels between the High nutrients and Low nutrients

treatments were small (less than 33%). This is especially small when it is recognized that the nutrient concentration of the Low nutrient treatments were 15 times lower. This effect was incorporated in the model by changed phosphorous concentration of chlorophyll with Low or High nutrients, and consequently the predicted chlorophyll levels by the model are more in accordance with the measured values, but it also suggest that phytoplankton can change its phosphorus uptake under different nutrient conditions.

Furthermore photoinhibition is not very often of importance under natural light conditions (Figure 3.8, high light treatments), only the first 2 days of the high light treatments showed clear effects of photoinhibition.

Overall the model results indicated that the phytoplankton of the treatments with high nutrient conditions was light-limited and that, both light and nutrients, limited the growth of the low nutrient treatments, with the exception of the LL treatment, which was light-limited.

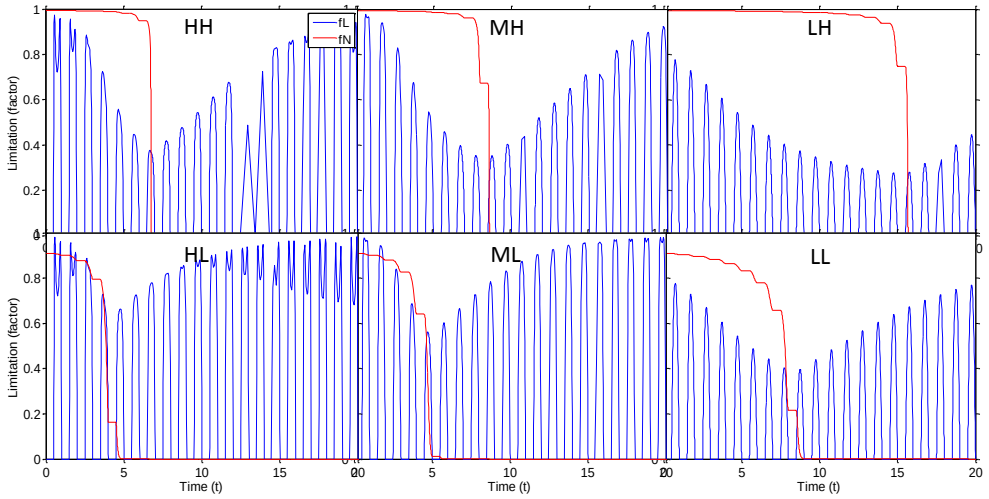

Figure 3.8 **Modelled limiting effects of nutrients (red) and light (blue) for each treatment of the Light & Nutrient experiment. For description of the different treatments and symbols see Table 2.1.**

3.4.2 Mwanza Gulf

The model predicts the maximum average chlorophyll levels of different mixing depths, these levels are only limited by light. In Figure 3.14 and Figure 3.13 these maximum chlorophyll levels for different phytoplankton loss rates are shown. The loss factor was changed in order to (partly)

correct the differences in phytoplankton death rate due to sinking, grazing and flushing between the experiment and the field. These factors were not present in the experiment and therefore the model predictions with higher loss factors (0.20 and 0.25) are displayed as well. If the chlorophyll levels of the field measurements fell between these boundaries, they were assumed to be light limited. In Figure 3.14 and Figure 3.13 these field values are shown besides the model results, with data labels for the different stations and different sampling dates respectively. Phytoplankton growth was light limited at least once for each station, suggesting that the maximum chlorophyll levels as predicted by the model were indeed the maximum levels. Furthermore the data points showed huge deviation, which can partly be explained by uncertainty about the correctness of the defined mixing depths. Since the used method to define mixing depths is depended on temperature differences, which are very small in a tropical lake, this is visible in the large standard deviations of the samples (see appendix 1). For example, station 4 showed huge differences in mixing depths between the different measurements (Figure 3.14). However the data points for station 3 and 4 at the right end of Figure 3.14 did not have large standard deviation for the defined mixing depth. These large values are probably explained by large differences in light attenuation between each sampling station and between different times of the year for a single station, altering maximum chlorophyll levels (see Figure 3.9). Part of the higher light attenuation for the most inshore station, number 1, was caused by higher chlorophyll levels, but this cannot explain all the difference (see Figure 3.10). Consequently this influences the model results, because parameters for the background light attenuation (k_d) and light attenuation of phytoplankton (k_a) were determined from all these measurements, therefore these values for the model parameters are likely too low for station 1 and possibly also for station 2 and vice versa for station 4 and station 3 respectively. This could be the reason why station 1 and 2 are often not close to the predicted values for light limitation. Moreover, seasonal differences for the different stations are large, light limited phytoplankton growth seems to occur most often in April and September and least often in October, November and December (Figure 3.13).

Some model parameters were changed in order to test the sensitivity of the model. Changing the amount of nutrients (Nu) did not lead to other predicted chlorophyll levels (see Figure 3.11) . Also the model was not very sensitive to changes in the light curve parameters (I_k and I_{opt}) (Figure 3.11). However the model was very sensitive to variations of the background turbidity and light attenuation of phytoplankton (Figure 3.12).

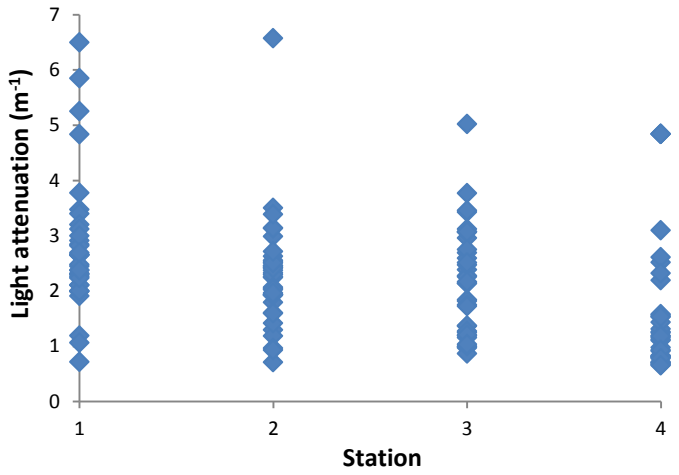

Figure 3.9 Light attenuation of all light attenuating components in the water column per station, for all measurements. Light attenuation is consisting of attenuation by phytoplankton biomass and background attenuation.

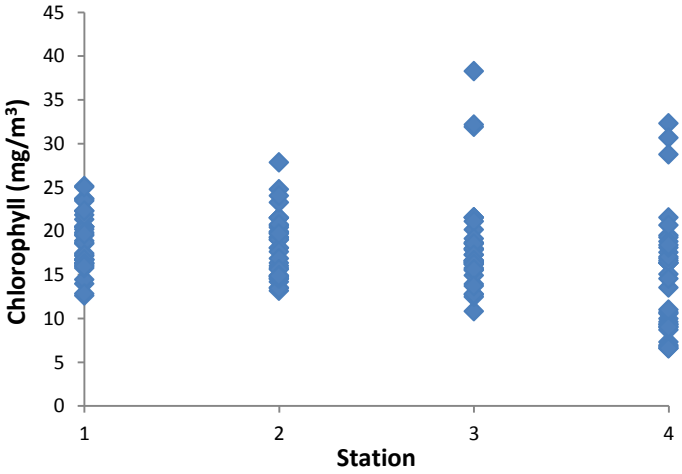

Figure 3.10 Average chlorophyll *a* concentrations (mg/m^3) over mixing depth per station, for all measurements.

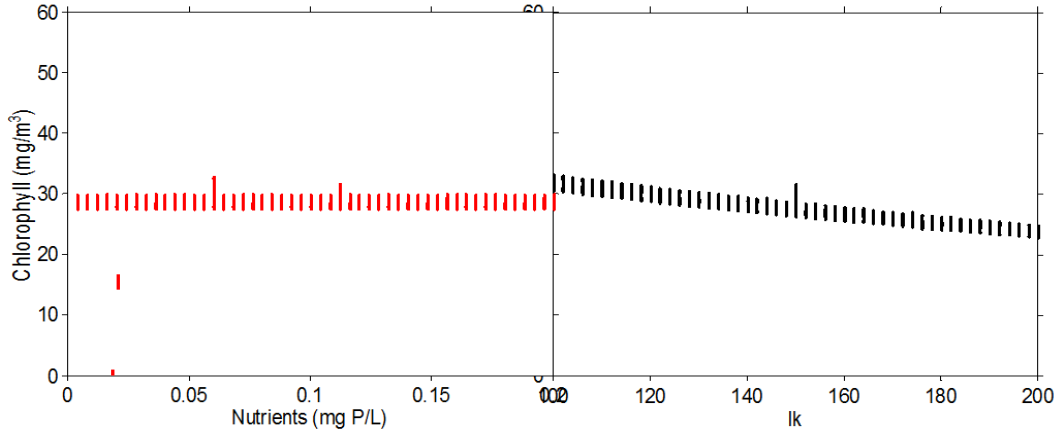

Figure 3.11 Sensitivity analysis for the parameters Nu (left) and I_k (right, in µE m^{-2} s^{-1}). Note that that $I_{opt} = 2 \cdot I_k$. Model calculations with 'standard' parameter settings, only the parameter on the x-axis is varied .

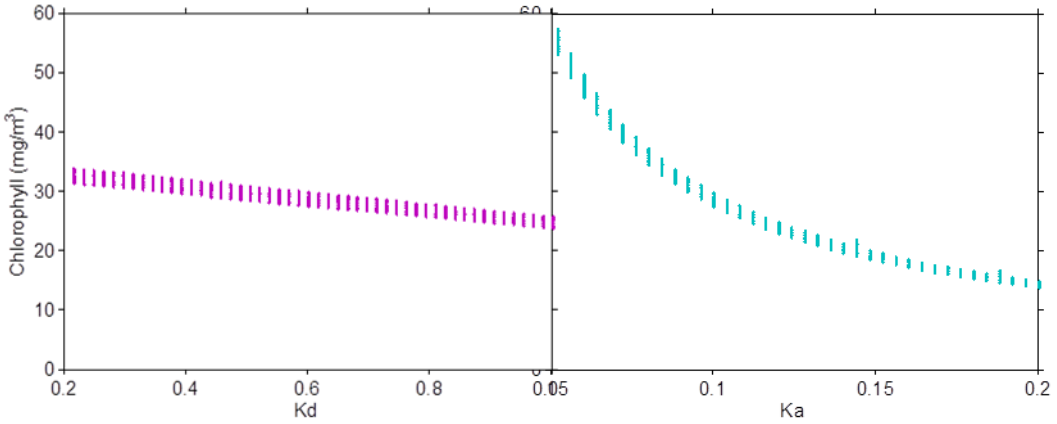

Figure 3.12 Sensitivity analysis for the parameters Kd (left, in m^{-1}) and Ka (right, in m^2 mg Chl a^{-1}). Model calculations with 'standard' parameter settings, only the parameter on the x-axis is varied .

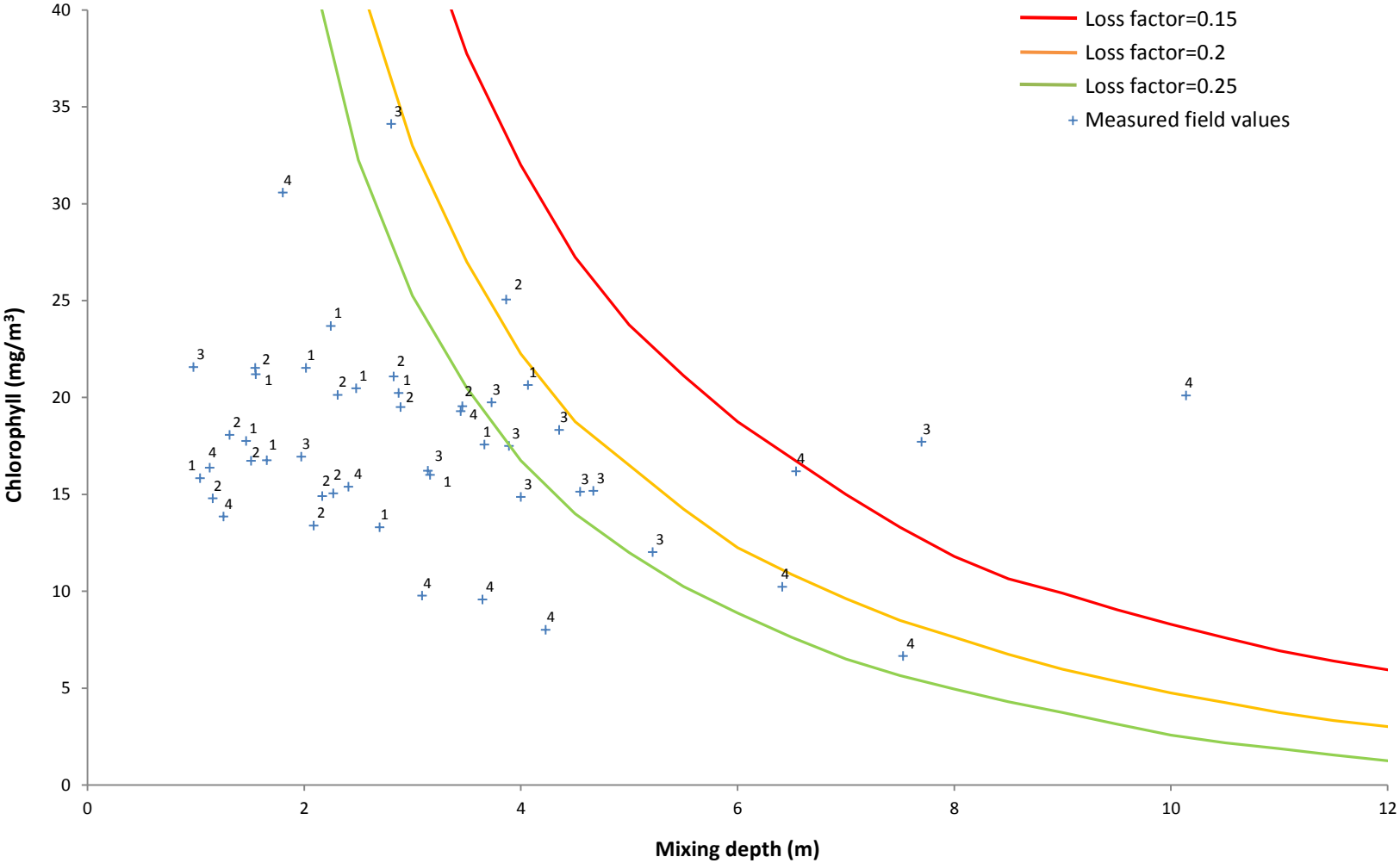

Figure 3.13 Model results for maximum chlorophyll level per mixing depth with different loss factors (red 0.15, orange 0.2 and green line 0.25) and measured values per station (number). See text for more detail.

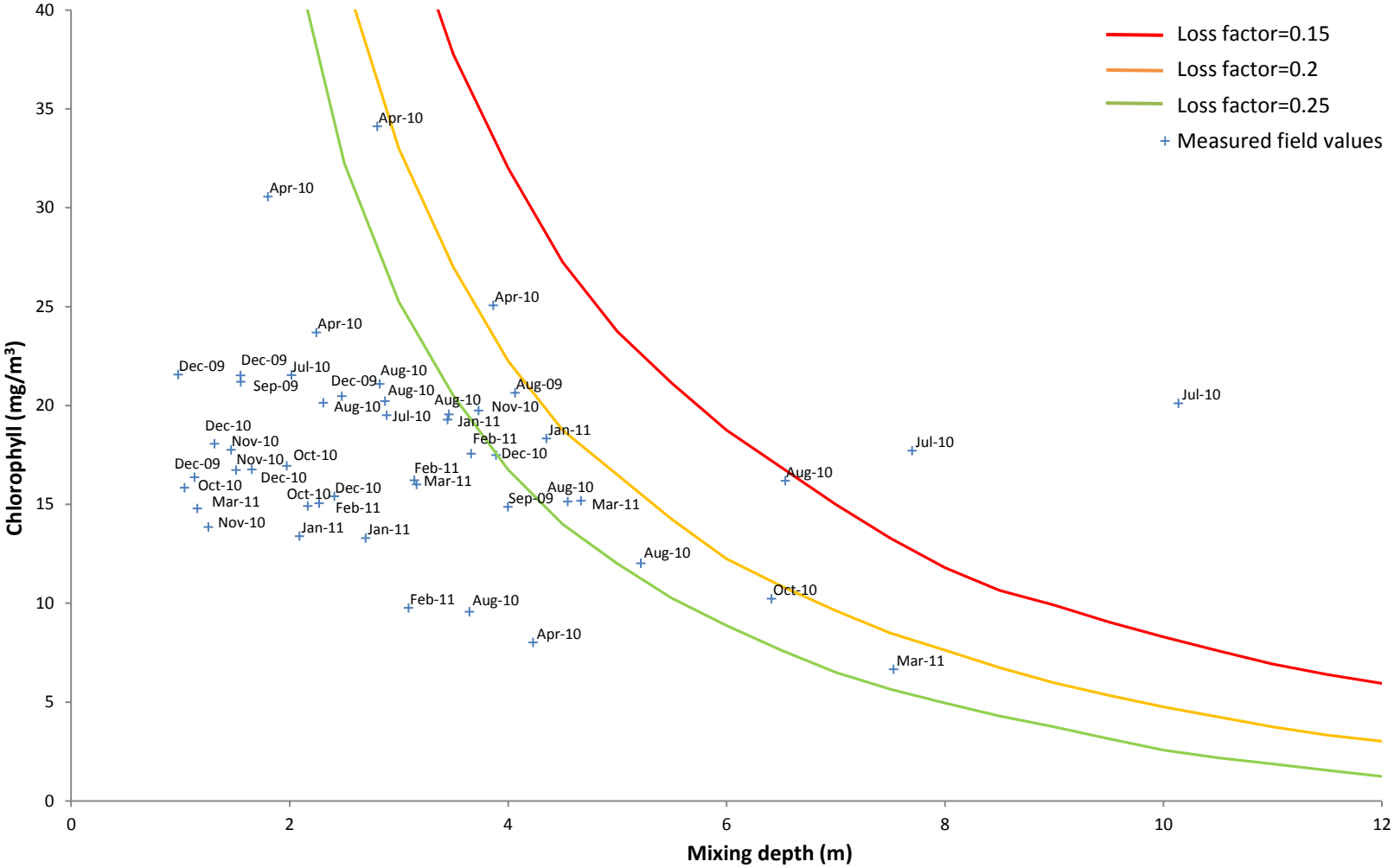

Figure 3.14 Model results for maximum chlorophyll level per mixing depth with different loss factors (red 0.15, orange 0.2 and green line 0.25) and measured values per date. See text for more detail.

4. Discussion

The phytoplankton community responded differently to the different treatments in all the three experiments. Algal biomass increased when they received higher amounts of nutrients (Nutrients experiment, Figure 3.1), the algae community was nitrogen-limited (N:P ratio experiment, Figure 3.3) and limited for light or nutrients (Light & Nutrients experiment, Figure 3.5). Cyanobacteria biomass did not show a clear response to the manipulated conditions.

4.1 Nutrients experiment

In the first experiment the chlorophyll levels changed synchronically with nutrients, the more nutrients added, the more chlorophyll was measured. But the development of cyanobacterial abundance did not show the same pattern. For the three treatments, were nutrients were added, the biomass of cyanobacteria was approximately the same, and thus the relative abundance of cyanobacteria decreased with higher nutrient concentrations. This was different from the hypothesis that cyanobacteria would dominate with high nutrient conditions. Indeed, in Lake Victoria a relationship between cyanobacteria abundance and nutrient levels is visible. The applied nutrient conditions were expected to promote cyanobacteria. Possibly the N:P ratio was still too high to cause a proliferation of cyanobacteria, because the N:P ratio of the nutrient additions was 15:1 and close to the Redfield ratio for optimum phytoplankton growth. Another possibility is that the relationship between nutrients and cyanobacteria is not *that* straightforward, more nutrients do not absolutely lead to higher cyanobacterial dominance (Sondergaard et al. 2011). Furthermore, the cyanobacteria biomass can also be explained by the duration of the experiment, which could have been too short for cyanobacteria to increase in abundance, because colony forming cyanobacteria are in general slow growing (Reynolds 2006). Besides they could have been outcompeted by other algae, such as green algae, because of their slow growth. Also the chaotic behavior of phytoplankton can be an explanation, which makes it complicated to predict phytoplankton community structures (Beninca et al. 2008).

4.2 N:P ratio experiment

In this experiment the nitrogen to phosphorus ratio was changed through nutrient additions. The statistical results proved that there was nitrogen limitation for the low treatment (Table 3.3, N:P ratio of 5:1). The medium and high treatment were not significantly different, thus (clear) nitrogen limitation did occur at N:P ratios smaller than 10:1. Which is a factor 10 smaller than the ratio of 20:1 that Guildford and Hecky (2000) found for which nitrogen limited growth could occur. This difference in ratio for which nitrogen limitation occurs could be attributed to the growth of N-fixing cyanobacteria in the experiment. By fixing atmospheric-N they could have raised the N availability and decrease nitrogen limitation for their growth. Unfortunately, this effect couldn`t be tested, because there is no data of the nutrient concentrations during the experiment. Nevertheless, if N-fixing cyanobacteria increased, the N availability in this experiment should also have increased. Indeed, cyanobacteria increased in absolute and relative abundance with higher N:P ratios, but the increase in relative abundance was less obvious (Figure 3.4). However there is no data on the abundance, relative or absolute, of N-fixing cyanobacteria, and since there are also no measurements of nutrient concentrations during the experiment, it is not possible to conclude that N-fixing cyanobacteria have increased and that cyanobacteria caused an increase in the total nitrogen concentrations.

However the increase of cyanobacteria with higher N:P ratio is in contrast with the assumption that low N:P ratios promote cyanobacteria (Schindler 1977, Smith 1983, Smith and Bennett 1999), because they can fix atmospheric nitrogen. This assumption is influential, but it is heavily debated (Trimbee and Prepas 1987, Downing et al. 2001, Kosten et al. 2009). Kosten et al. (2009), found no correlation between cyanobacteria and low N:P ratios or low N concentrations along (sub)tropical lakes in south America and Downing et al. (2001) concluded from their analysis of 99 lakes around the world that cyanobacterial dominance is more closely related to the amounts of nutrients or algae biomass. The results of the N:P ratio experiment indicate that low N:P ratios not necessarily lead to higher abundance of cyanobacteria, which confirms previous findings by other authors (Jensen et al. 1994, Kosten et al. 2009).

However, in contrast to the N:- ratio experiment where with more nutrients the cyanobacteria abundance increased, high nutrient loadings of the Nutrients experiment, did not result in higher abundance of cyanobacteria . This is contrasting with findings of other authors that cyanobacteria is more related to (high) nutrient concentrations than low N:P ratios (Downing et al. 2001). Other factors, such as the presence or absence of species, weather conditions, anoxic

conditions, flushing rate and presence and abundance of grazers (Anderson et al. 2002), are also of influence on the growth and dominance of cyanobacteria. This could be an explanation, if these factors contributed to the experiment, but because the experiments (N:P ratio, Nutrients and Light & Nutrients) were conducted in the same period with similar conditions, except for the nutrient additions, and without many of these above noted confounding factors , these effects are likely to be limited. Also iron (Fe) could limit phytoplankton growth, but research by Guildford et al. (2003) did not find a limited effect of this micronutrient for Lake Victoria. Therefore it is not expected that Fe would play a role.

4.3 Light & Nutrients experiment

The Light & Nutrients experiment clearly shows light and nutrient limitation. The six different treatments, the control treatment put aside, show the theoretical expected reaction on the light and nutrient conditions (see Figure 3.5). Further analysis with a mini-model confirmed this picture; phytoplankton is light-limited under high nutrients concentrations and nutrient and light-limited with low nutrient concentrations, with the exception of the LL treatment (Figure 3.7), which is only light-limited.

Furthermore, the model points to the effect that photoinhibition can have on the growth of phytoplankton under natural light conditions. In the first two days of the experiment the model indicates that the natural light treatment is more light-limited than the 50% light treatment. This is due to photoinhibition, because phytoplankton biomass is almost the same (see also Figure 3.8). After these days the effect of photoinhibition is reduced by self-shading of phytoplankton.

The analyses with the mini-model also suggest that the relatively small differences between the chlorophyll levels of the two nutrient treatments of the Light & Nutrients experiment could be explained by the capability of phytoplankton to change their nutrient stoichiometry. The low nutrient treatments, with a 15 times smaller nutrient load than the high nutrient treatments, had 30% lower chlorophyll levels at most. This suggests that the phytoplankton of the low nutrient treatments need a smaller amount of nutrients for the same amount of chlorophyll. A study by Hall et al. (2004) showed similar effects. However, the modelled results were not completely in line with the Light:Nutrient hypothesis, which predicts that Light:Nutrient ratios are the driven factor for the Carbon(C):nutrients ratios. High light or low P concentrations could lead to high C:P ratios, for example (Reynolds 2006). But the generally observed decrease of

C:Chl ratios with lower light (Healey 1985, Hall et al. 2004, Reynolds 2006) and the lack of measured nutrient stoichiometry parameters of the experiment, made it difficult to disentangle the different effects of nutrient and light on the stoichiometry of phytoplankton in this experiment. However, the results point to the effect that the availability of nutrients can have on phytoplankton's nutrients stoichiometry and this probably explains the small differences in chlorophyll levels between the high and low nutrient treatments.

Cyanobacteria abundance was higher when treated with more light and nutrients (Table 3.6), but the relative abundance did not increase, except in the MH treatment. Therefore, the cyanobacterial dominance of the different treatments gave no indication that cyanobacteria were promoted under low light conditions, although increasing cyanobacterial dominance was expected. Because some groups of cyanobacteria are more shade tolerant than other algae and some can regulate their buoyancy to maintain their position near the surface. This is beneficial, because they take away the available light for other phytoplankton species lower in the water column (Reynolds 2006). However these effects were not visible in the experiments.

4.4 Links to lake Victoria

Caution is needed when linking results of mesocosms studies to the field, because several processes could gain inappropriate high rates (Carpenter 1996). For this reason chlorophyll levels reached such high values in this study, which are not unusual for mesocosm and microcosm experiments (Svensen et al. 2002), but are unnatural high for a natural lake. Therefore, the relative responses of the experiments, such as the effects of different N:P ratios, and not the exact rates have to be linked to the field. When these artifacts are taken into account, mesocosms as experimental ecosystems that can be conducted under replicate, controlled and repeatable conditions, are a useful tool (Drake et al. 1996).

The eutrophication experiments gave a complicated picture of the effects of higher nutrient loadings and changed N:P ratios on the phytoplankton composition; cyanobacterial dominance did not show an unambiguous increase along a eutrophication gradient. Cyanobacterial dominance did not increase with more nutrients, but with higher N:P ratios. Cyanobacteria are the dominant phytoplankton group in the eutrophic lake Victoria and increased eutrophication is expected to be beneficial for cyanobacteria (Kling et al. 2001), but in this study there is no clear stimulating effect of eutrophication on the dominance of cyanobacteria. It rather indicates that

eutrophication is not the only mechanism, although important, that explains dominance of cyanobacteria (Jensen et al. 1994, Anderson et al. 2002, Kosten et al. 2009).

The eutrophication process of Lake Victoria has resulted that light being nowadays the most important limiting factor for phytoplankton growth, instead of nitrogen, for both the inshore and offshore areas (Mugidde 2001, Silsbe et al. 2006, Hecky et al. 2010). However Lake Victoria remains a nitrogen deficient system compared to other freshwater lakes (Guildford and Hecky 2000), which is visible in the low N:P ratios offshore of 12:1 with higher N:P ratios of 35:1 reported inshore (Mugidde 2001). These ratios are attributed to high N-fixation of cyanobacteria (Hecky et al. 2010). Cyanobacteria are not dependent on nitrogen for they can fix atmospheric nitrogen, and therefore total N:P ratios (TN:TP) can be high, while the phytoplankton which are not able to fix nitrogen are N-limited, as showed by nutrient experiments for the shallow parts of the lake (Lehman and Branstrator 1994, Guildford et al. 2003, North et al. 2008). This study indicates that obvious N-limited growth of phytoplankton seems to start at N:P ratios of 10:1. The average N:P ratio of the inshore water of the Mwanza gulf is around 25:1, ranging from 12:1 to 46:1 from deep to shallow depths (Cornelissen unpubl. data). N:P ratios can give an indication if an aquatic system is more N- or P-limited. Guildford and Hecky (2000), found that (severe) N-limitation occurs at total N:P ratios smaller than 20:1 and (severe) P-limitation at ratios larger 50:1 for a broad range of lakes and oceans. Kosten et al. (2009), found ratios of smaller than 20:1 for N-limitation and larger than 38:1 for P-limitation for 83 shallow lakes in South America. These ranges for N and P limitation indicate that the phytoplankton in the Mwanza Gulf, if light is sufficient, is probably not severely limited by N, but is experiencing rather small limitation effects of N or could even be limited by P. However a recent nutrient enrichment experiment did not found indication of P-limitation in shallow areas of Lake Victoria. Phytoplankton was primarily limited by N when light was sufficient (North et al. 2008).

Nitrogen is probably the most limiting *nutrient*, but the experiments suggest that light limits phytoplankton to the greatest extent. Because the chlorophyll levels of all the three control treatments of the experiments increased after the start of the experiment, while no factors changed and no nutrients were added to these treatments, indicating that growth was light limited *in situ* (see also Figure 4.1). Guildford et al. (2003) found a similar effect in their nutrient enrichment experiments. Other studies also indicate that light is the primary limiting factor for phytoplankton growth in inshore areas (Gikuma-Njuru and Hecky 2005, Silsbe et al. 2006, Loiselle et al. 2008).

However, the model results did not unambiguously indicate that phytoplankton growth in the Mwanza Gulf is limited by light. Some of the measured field values were within the borders of the predicted maximum chlorophyll levels, where phytoplankton growth is limited by light. However a large proportion of the measurements were not at this chlorophyll level, indicating that other factors than light limits phytoplankton growth. The standard deviations of some of the field measurements were large, but even with the most favorable values there were many occasions that the measurements were not between the borders for which the model predicts light limited phytoplankton growth. The model results rather point to other factors that limit phytoplankton growth, such as background extinction or nutrients. The measured nutrient concentrations in the Mwanza Gulf (Cornelissen unpubl. data, Shayo et al. 2011) were in the same range as in other parts of the lake (Gikuma-Njuru and Hecky 2005, Silsbe et al. 2006) and do not indicate that phytoplankton is nutrient limited in the gulf. Moreover, the average chlorophyll levels in the Mwanza Gulf are in general lower than in other parts of the lake, where phytoplankton growth is light limited (Gikuma-Njuru and Hecky 2005, Silsbe et al. 2006, Loiselle et al. 2008). Furthermore, nitrogen is the most limiting nutrient in Lake Victoria (Lehman and Branstrator 1994, North et al. 2008, Hecky et al. 2010), and thus probably also in the Mwanza Gulf. However, it is assumed that it is not likely that phytoplankton growth is limited by nitrogen, because the phytoplankton of inshore waters is dominated by cyanobacteria, which probably overcome N-deficiency in the water column by fixing atmospheric-N (Hecky et al. 2010).

Therefore, phytoplankton is probably limited by light due to the high light extinction in the Mwanza Gulf (Figure 3.9), for which the model results are very sensitive (Figure 3.12). This high light extinction in the Mwanza Gulf is caused by high concentrations of dissolved organic and inorganic matter, and decreases from shallow to deep areas (Cornelissen, in prep.). Decreasing light extinction from deep(er) to shallow water is also visible in Figure 3.9. These high concentrations are caused by slow flushing of and high wastewater inputs from channels and streams to the Mwanza gulf (Machiwa 2010). Furthermore the sediment of the Mwanza Gulf consists of mud, especially in the shallow areas where sediment is easily resuspended, probably contributing to light extinction.

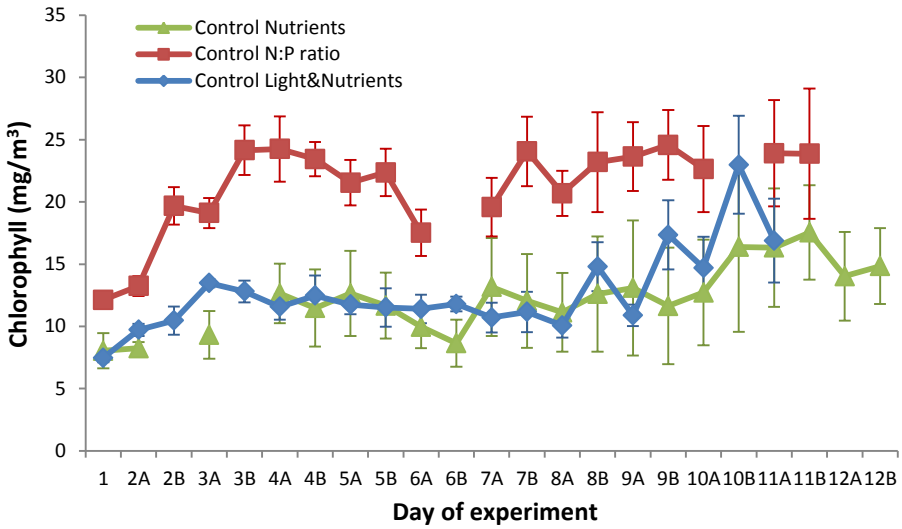

Figure 4.1 **Chlorophyll levels of the control treatments of the three experiments. The x-axis shows the day of the experiment, A = morning and B = afternoon measurement. No nutrients were added to these control treatments.**

Seasonal differences of both chlorophyll levels and mixing depth were large for the different stations; phytoplankton growth was limited by light or far away from the predicted values for which growth was light limited. This large deviation is probably the result of the shallowness of the water where the measured stations were located. Consequently the water column is frequently completely mixed, which is wind induced and occurs approximately once in the two or three days, throughout the year (Mugidde 2001, Silsbe 2004). The shallow depths of inshore areas and the associated frequent mixing of the entire water column removes the main mechanisms which are responsible for the phytoplankton seasonality offshore; nutrient recycling and differences in mixing depths (Silsbe et al. 2006). This frequent complete mixing leads to higher background extinction by resuspension of organic and inorganic matter, resulting in phytoplankton growth that is more strongly limited by light. It could also explains the distance of station 1 and 2 to maximum chlorophyll levels. Research by Silsbe et al. (2006), confirmed that wind speed is an important factor for inshore areas, chlorophyll and average water temperature were positively correlated with wind speed. Concluding, the driving factor for the seasonal differences is probably wind induced resuspension, rather than seasonal differences. The observed seasonality therefore probably reflects differences in wind induced mixing.

There is increasing evidence that many parts of Lake Victoria, both inshore and offshore, are light-limited . Mugidde (1993) was one of the first to suggest that the phytoplankton community is at least in parts of the lake light-limited through self-shading of algae. Silsbe et al. (2006) gave more evidence in their thorough study. This study also indicates that phytoplankton growth in the Mwanza Gulf is probably light limited due to high background extinction. This high background extinction is caused by high attenuation of suspended organic and inorganic matter (Cornelissen, in prep). Therefore it is expected that further increase in nutrient concentrations in the Mwanza Gulf will not lead to an increase of primary production.

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Appendices

Appendix 1: Measured values of the field stations and graphical representation

Table I Measured values of mixing depth and chlorophyll level and the standard deviation for these measurements for the four stations per date. Note: each sample is graphically displayed with the model results for maximum chlorophyll level in the graph below.

Sample	Date	Station	Mixing Depth (m)	Chlorophyll (mg/m3)	St. dev. Mixing depth (m)	St. dev. Chlorophyll (mg/m^3)
1	Sep-09	3	4.00	14.87	0.92	0.46
2	Apr-10	4	4.23	8.01	0.96	2.12
3	Aug-10	2	2.83	21.08	3.41	1.62
4	Sep-09	1	1.55	21.19	2.59	0.17
5	Dec-09	1	2.48	20.47	0.00	0.00
6	Dec-09	2	1.55	21.52	0.00	0.00
7	Dec-09	3	0.98	21.56	0.00	0.00
8	Dec-09	4	1.13	16.37	0.00	0.00
9	Apr-10	3	2.80	34.11	3.60	0.73
10	Apr-10	1	2.25	23.69	1.43	0.55
11	Apr-10	2	3.87	25.06	2.45	1.83
12	Apr-10	4	1.80	30.56	1.78	0.27
13	Jul-10	3	7.70	17.71	1.06	0.10
14	Aug-09	1	4.07	20.63	1.07	0.51
15	Jul-10	2	2.89	19.50	0.38	0.65
16	Jul-10	4	10.14	20.10	1.25	0.30
17	Aug-10	1	2.02	21.52	4.76	0.89
18	Aug-10	2	3.46	19.54	0.49	1.75
19	Aug-10	3	5.22	12.01	1.02	2.46
20	Aug-10	4	6.54	16.18	0.98	3.06
21	Aug-10	1	2.87	20.22	1.84	0.52
22	Aug-10	2	2.31	20.13	0.93	1.31
23	Aug-10	3	4.55	15.13	2.01	1.10
24	Aug-10	4	3.65	9.57	0.46	0.85
25	Oct-10	1	1.04	15.83	1.60	0.06
26	Oct-10	2	2.17	14.90	0.98	1.36
27	Oct-10	3	1.97	16.94	0.90	0.60
28	Oct-10	4	6.41	10.22	0.74	1.95
29	Nov-10	1	1.47	17.75	0.80	0.19
30	Nov-10	2	1.51	16.73	1.20	0.32
31	Nov-10	3	3.73	19.74	1.60	2.40
32	Nov-10	4	1.26	13.85	5.99	0.16
33	Dec-10	1	1.66	16.75	0.46	0.50
34	Dec-10	2	1.31	18.06	1.46	0.56
35	Dec-10	3	3.89	17.49	1.01	1.83
36	Dec-10	4	2.41	15.40	2.40	0.50
37	Jan-11	3	4.35	18.32	0.95	1.22
38	Jan-11	4	3.45	19.28	1.22	0.63
39	Jan-11	1	2.70	13.29	0.99	1.05
40	Jan-11	2	2.09	13.38	0.20	1.04
41	Feb-11	1	3.66	17.56	1.82	0.33
42	Feb-11	2	2.27	15.05	0.50	1.17
43	Feb-11	3	3.14	16.21	0.61	2.36
44	Feb-11	4	3.09	9.76	1.10	2.48

Sample	Date	Station	Mixing Depth (m)	Chlorophyll (mg/m3)	St. dev. Mixing depth (m)	St. dev. Chlorophyll (mg/m^3)
45	Mar-11	1	3.16	16.00	0.26	1.53
46	Mar-11	2	1.16	14.79	0.20	0.16
47	Mar-11	3	4.67	15.18	1.31	2.94
48	Mar-11	4	7.53	6.66	0.12	3.23

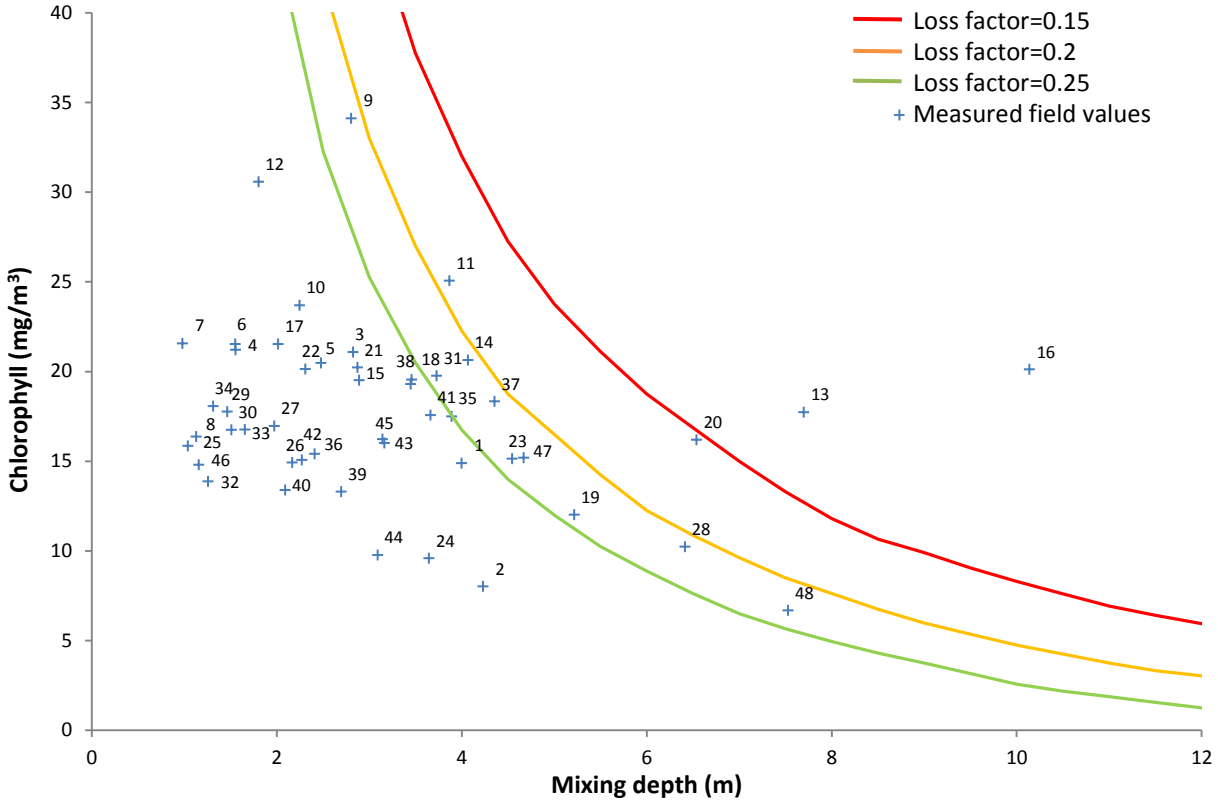

Figure I Model results for maximum chlorophyll level per mixing depth with different loss factors (red 0.15, orange 0.2 and green line 0.25) and measured values per measurements (number). See paragraph 3.4 for more detail.

Appendix 2: Model equations

Light & Nutrient experiment Model

Model equations;

fL=(2*Iin*(atan(Iin*(2*Iin*Az+Bz)/sqrt(Iin^2*(-Bz^2+4*Az*Cz)))-atan(Iin*(2*Iin*Az*exp(-d*(Kd+A*Ka))+Bz)/sqrt(Iin^2*(-Bz^2+4*Az*Cz))))/(d*(Kd+A*Ka)*sqrt(Iin^2*(-Bz^2+4*Az*Cz))))

fNu=Nu/(Nu+k)

A'=(Pmax*A*(min(fL,fN)))-l*A

Nu'=-g*Pmax*A*(min(fL,fNu))

Az=(Ik/(Iopt^2))

Bz=(1-(2*(Ik/Iopt)))

Iin=RED*(Imax*iif(sin(2*pi*t-pi)>0,sin(2*pi*t-pi),0.00000000000000000000000000000000000001))

Parameter values

Pmax=2;

Iopt=270;

Iopt2=270;

Ik2=135;

Ik=135;

A=8;

Imax=955;

k=0.005;

N=0.75;

g=0.004;

d=0.5;

Kd=0.6;

l=0.15;

Ka=0.1;

RED=1;

Mwanza Gulf model

Model equations

fL=(2*Iin*(atan(Iin*(2*Iin*Az+Bz)/sqrt(Iin^2*(-Bz^2+4*Az*Cz)))-atan(Iin*(2*Iin*Az*exp(-d*(Kd+A*Ka))+Bz)/sqrt(Iin^2*(-Bz^2+4*Az*Cz))))/(d*(Kd+A*Ka)*sqrt(Iin^2*(-Bz^2+4*Az*Cz))))

fNu=Nu/(Nu+k)

A'=(Pmax*A*(min(fL,fNu)))-l*A

Az=(Ik/((2*Ik)^2))

Bz=(1-(2*(Ik/(2*Ik))))

Cz=(Ik)

Iin=RED*(Imax*iif(sin(2*pi*t-pi)>0,sin(2*pi*t-pi),0.00000000000000000000000000000000000001))

Parameter values

Pmax=2;

Iopt=270;

Ik=135;

A=8;

Imax=955;

k=0.005;

Nu=0.1;

g=0.004;

d=25;

Kd=0.6;

l=0.15;

Ka=0.1;

RED=1;