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**THE EFFECTS OF LAND USE CHANGE ON LITTORAL ZONE DYNAMICS OF  
LAKE TANGANYIKA, EAST AFRICA**

by

Catherine Marie O'Reilly

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A Dissertation Submitted to the Faculty of the

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In Partial Fulfillment of the Requirements  
For the Degree of

**DOCTOR OF PHILOSOPHY**

In the Graduate College

**THE UNIVERSITY OF ARIZONA**

2001

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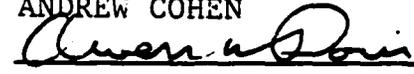
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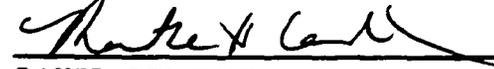
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**'Before me – untrodden Africa; against me – the obstacles that had defeated the world since its creation; on my side – a somewhat tough constitution, perfect independence, a long experience in savage life, and both time and means which I intended to devote to the object without limit.'**

**– Samuel Baker, "The Albert N'yanza", 1866**

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## **ABSTRACT**

Lake Tanganyika, East Africa, is one of the world's unique freshwater ecosystems. This lake is approximately 10 million years old and contains an extremely diverse fauna with high levels of endemism. Most of the biodiversity in the lake is concentrated along the rocky shoreline, and this dissertation focused on the land-water interactions that may affect the littoral ecosystem as human population densities increase.

First, the potential of carbon and nitrogen stable isotopes as indicators of human impact was examined. Sedimentary organic matter from four river deltas with contrasting patterns of land use was used to develop a predictive relationship between terrestrial patterns and geochemical signals. Stable isotope analyses of cores taken at two disturbed and two undisturbed watersheds were consistent with patterns seen in surface sediments. These results suggest that nitrogen isotopes are a better indicator of land use while carbon isotopes are useful in determining changes in vegetation patterns.

To evaluate the effect of deforestation on ecosystem dynamics, epilithic metabolism was measured at several sites over a period of one year. Epilithic net productivity did not differ significantly between the disturbed and undisturbed watersheds, but epilithic respiration and algal biomass were significantly higher at the disturbed site. Further evidence of disturbance was given by greater amounts of inorganic material on the rocks and lower ambient oxygen concentrations at the impacted site.

Finally, in order to identify species more susceptible to changes in benthic productivity, the food web structure of the pelagic and littoral food webs was elucidated

using stable isotopic analyses. Diet specificity is not apparent in the littoral food web, suggesting that broad dietary preferences may help stabilize this persistent food web during environmental perturbations. The isotopic structure of the pelagic food web suggests that upwelling of deeper waters is an important nutrient source for the food web, which is consistent with current nutrient and hydrodynamic models.

## **CHAPTER 1: INTRODUCTION**

### **Statement of Problem**

The objective of my research is to increase our understanding of how human impacts affect lake ecosystems and to improve our ability to predict the outcome of anthropogenic disturbances. Watershed destruction, species introductions, and overfishing are interacting disturbance factors that place the environmental health of aquatic systems at risk. Changes in land use patterns are perhaps the most ubiquitous problems, leading to increases in nutrient, sediment, and pollutant inputs. Collectively, these alter productivity and biodiversity, reduce available habitat, and poison food resources. Our attempts to control and manage these disturbance factors are restricted by our limited knowledge of the changes they induce in lakes.

The focus of my dissertation is Lake Tanganyika, East Africa, which faces rapid, unregulated demographic changes and the potential destruction of one of our most unusual aquatic ecosystems. Lake Tanganyika is a large (length 650 km, mean width 50 km, mean and maximum depths 570 m and 1470 m respectively) rift valley lake located just south of the equator (Coulter and Spigel 1991). It is oligotrophic and permanently stratified, with periodic localized upwellings of deep nutrient-rich water occurring during the dry-windy season.

The great age of this lake (approx. 10 million years) has allowed for extensive evolution of many faunal groups and the development of one of the world's most biologically diverse freshwater ecosystems (Coulter 1991). The pelagic zone contains a

simple, species-poor community, which has several links to the littoral zone through feeding and breeding. In contrast, the littoral communities are highly diverse, with over 1400 species (Coulter 1991). Species flocks with high levels of endemism are the cichlid and non-cichlid species, mollusks, and invertebrate crustaceans.

Human population growth rates in this region are as high as 3.15% per annum (CIA 2000), and increases in population density are associated with changing land use patterns. Throughout the region, land is cleared primarily to provide fuel wood and for agriculture. Deforestation approaches 100% in the north and 40 to 60% in the central area of the lake watershed (Cohen et al. 1993). Small farms are cultivated on steep slopes along the rift valley escarpment, with minimal efforts to control erosion. Soil erosion rates in steeply sloping, intensively cultivated areas in the north of the watershed range from 28 to 100 metric tons  $\text{ha}^{-1} \text{yr}^{-1}$  (Bizimana and Duchafour 1991). Refugee activity during the last several years has likely placed additional resource demands on both the land and the lake.

The greatest threats to the lake are nutrient and sediment inputs from increasing deforestation and watershed development (Cohen et al. 1996). Initially, these inputs affect the littoral zone, which houses most of the lake's diversity. Changes in absolute and relative concentrations of nutrients can affect primary productivity rates and algal community composition. Sediment inputs reduce light penetration, which also affects algal growth, and fill in crevices in rocky areas that may serve as predatory refugia or habitat. The littoral zone serves as grounds for breeding or habitat during the juvenile stage for many pelagic fish species, which are economically important for the region. The negative impact of increased turbidity on species diversity has already been

documented for Lake Victoria (Seehausen et al. 1997), and recent work suggests that deforestation may also be having a negative impact on biodiversity in Lake Tanganyika (Alin et al. 1999).

This study takes two approaches to assessing the impact of land use change on Lake Tanganyika. First, it attempts to link changes in land use directly to the aquatic environment using stable isotope tracers. Carbon isotopes were used to examine vegetation patterns while nitrogen isotopes indicated land use (such as deforestation and cultivation) and were related to population densities. Together, carbon and nitrogen isotopes and carbon: nitrogen ratios provide an efficient method to determine the source of organic material in the lake and have proven useful in detecting human impacts on other aquatic systems (Kendall 1998; Fry 1999; Tucker et al. 1999). In addition, this study will allow for more accurate interpretations of paleolimnological isotopic signals in Lake Tanganyika.

Secondly, this study evaluates the effect of deforestation on biological processes in the littoral and nearshore regions of the lake. The diverse littoral community is supported in part by benthic algae, and changes in algal productivity may have significant implications for the upper food web. Stable isotopic analysis of the littoral food web makes it possible to trace energy sources and to determine which species rely most heavily on benthic algae (and are thus most likely to be affected by changes in their food source). Since stable isotope analysis elucidates food web structure, this approach also provides insight as to the mechanisms that are important for the stability and resilience of these food webs.

## **Dissertation Format**

This dissertation consists of four separate manuscripts and one report, which appear as appendices. The first manuscript, *Geochemical signals in sedimentary organic matter reflect watershed land use and vegetation patterns*, compares stable isotopic signatures of sedimentary organic matter from several river deltas. These rivers drain a range of watershed sizes and disturbance levels. This manuscript will be submitted to *Limnology and Oceanography*.

The report, *Benthic algal productivity in Lake Tanganyika and the effects of deforestation*, was written for the United Nations Development Program/Global Environmental Facility Lake Tanganyika Biodiversity Project. This report was originally written as a Final Report after a year of working in Kigoma, Tanzania, and studying epilithic algal dynamics and the impact of deforestation on epilithic productivity. This original technical report may be downloaded from the project's web site (<http://www.ltbp.org>) or is available by request from the project or the author. This report will be written as a manuscript, possibly incorporating other data from some of the study sites in collaboration with Simone Alin. The manuscript, *Seasonal dynamics of periphyton in a large tropical lake, Lake Tanganyika, East Africa*, examines seasonal variability in epilithic algal production, estimates lake-wide benthic productivity, and compares the results of this data set to a latitudinal gradient of similar lakes. This manuscript will be submitted to *Hydrobiologia*.

The last two manuscripts use stable isotope analyses of the littoral and pelagic food webs to examine nutrient inputs and food web structure. *Food web structure in the*

*littoral zone of Lake Tanganyika, East Africa: Insights from isotopic analyses* delineates the main energy sources and demonstrates that diet specificity does not appear to be an important characteristic of this food web. This manuscript will be submitted to *Oecologia*. The other manuscript, *Interpreting stable isotopes in food webs: Recognizing the role of time-averaging at different trophic levels*, uses carbon and nitrogen isotopes to show evidence of upwelling and its importance as a nutrient source for the pelagic food web. This manuscript has been accepted as a Note for *Limnology and Oceanography*.

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## CHAPTER 2: PRESENT STUDY

The methods, results, and conclusions of this study are presented in the manuscripts appended to this dissertation. The following is a summary of the most important findings.

This study represents important research on the effect of land use change on aquatic systems. First, this dissertation examines the relationship between watershed size, land use patterns, and terrestrial inputs to Lake Tanganyika by comparing stable isotope ratios of organic matter in surface sediments of various river deltas. River delta sediments represent a temporally and spatially integrated archive of watershed conditions. Disturbed watersheds had significantly enriched carbon and nitrogen isotopes and higher carbon: nitrogen ratios. These results suggest that land use change introduces terrestrial organic matter, in the form of plant material, soil organic matter, and/or sewage, into the lake. The stable isotope signature is not only related to land use however, but watershed size is also a confounding factor, with larger watersheds having enriched carbon isotopes and higher carbon: nitrogen ratios. Larger watersheds are more subject to flood pulses during the wet season, which flush out organic particulate matter from soils. Understanding the differences in watershed hydrodynamics appears to be important in interpreting isotopic signal in the river deltas.

The surface sediment data set was used to calibrate data from sediment cores, and a recent (post 1850's) trend consistent with terrestrial inputs is clearly visible at the disturbed sites. Enrichment of nitrogen isotopic ratios can be correlated to changes in

human population densities, and recovery after the gazetting of Gombe Stream National Park is suggested in the core from that site. In contrast, carbon isotopic ratios become depleted after 1850 in all cores. This lakewide depletion in  $\delta^{13}\text{C}$  may be due to anthropogenic inputs of depleted carbon into the atmosphere through fossil fuel burning (the Suess effect). These studies of sediment geochemistry represent an important baseline for the interpretation of isotope signatures in paleolimnology.

This dissertation also provides the first substantial long term data on epilithic productivity in a tropical lake and how deforestation may be affecting benthic productivity. Seasonal variations in epilithic productivity appear to be related to lake hydrodynamics, with minimal changes in the northern area of the lake, but large differences in the southern area of the lake that correlate with upwelling during the dry-windy season. Disturbed shorelines have significantly higher algal respiration and lower biomass-specific net productivity, suggesting increased stress levels for benthic algae. The increased sediment input may extend feeding time or lower food quality for algal grazers, and gastropod and fish abundance and diversity was significantly lower at the disturbed site. Further evidence for terrestrial inputs exists as an increase in sediment on rock surfaces and as lower ambient oxygen concentrations in the water column at disturbed sites.

Finally, this study uses stable isotopic analysis of the littoral and pelagic food web to examine nutrient sources, energy flows, and community structure. Understanding these aspects of food web helps in assessing the impact of disturbance. Carbon isotopes indicate the proportion of the littoral food web that relies on benthic algae, which allows

identification of species most likely to be affected by changes in epilithic productivity. However, upper trophic levels of the littoral food web are primarily dependent on pelagic (phytoplanktonic) carbon, and several species relying on a mix of benthic and pelagic carbon, either by consuming a wide range of prey items or as detritivores. Although food resource partitioning exists on a gross scale (such as between gastropods and grazing fishes), functional redundancy among the fishes may be part of the reason for the high ecosystem resistance and resilience found among the nearshore fish community.

Stable isotopic analysis of the pelagic food web revealed that deepwater upwelling events during the windy season are an important nutrient source. Inputs of deepwater carbon and nitrate have distinct isotopic ratios, and these nutrients are rapidly taken up by phytoplankton. Although this isotopic signature also shows up in zooplankton, it does not appear in the fish species because their larger body mass integrates over a longer time period and does not reflect these short term upwelling events. This study demonstrates the importance of recognizing time integration at different levels in a food web.

## **APPENDIX A: GEOCHEMICAL SIGNALS IN SEDIMENTARY ORGANIC MATTER REFLECT WATERSHED LAND USE AND VEGETATION PATTERNS.**

### **Abstract**

Geochemical signals can provide information about both internal processes and terrestrial inputs to a lake. As such, they offer a powerful approach to detecting changes in aquatic systems related to climate or human impacts. We investigated the potential of carbon and nitrogen stable isotopes and carbon:nitrogen ratios to trace watershed vegetation patterns and land use changes by comparing sedimentary organic matter at several river deltas in Lake Tanganyika, East Africa.

We found that nitrogen isotopes were the best indicator of anthropogenic land use patterns. C:N ratios were useful in distinguishing between terrestrial and aquatic carbon sources, while carbon isotopes predominately reflected autochthonous material and were related only in part to watershed vegetation patterns. Our results further suggest that watershed size and the intensity of land use may be important factors in determining geochemical signals in lake sediments. Analyses of cores were consistent with patterns seen in surface sediments. Nitrogen isotopes changed commensurate with historical records of population growth. Carbon isotopic ratios suggest a decrease in lake productivity due to increased thermal stratification from global warming.

## Introduction

Biogeochemical signals are useful tools for studying both natural and anthropogenic changes in watersheds. Several studies have used carbon isotopes to demonstrate the links between watershed vegetation and particulate organic carbon (POC) in rivers (Martinelli et al. 1999), and that this vegetation signal is preserved in river sediments (Bird et al. 1994) and to a less defined extent in river delta systems (Mariotti et al. 1991; Bird et al. 1994). These studies have used carbon isotopes because they differentiate between C3 plants ( $-27\text{‰}$  to  $-29\text{‰}$   $\delta^{13}\text{C}$ ) and C4 plants ( $-12\text{‰}$  to  $-13\text{‰}$   $\delta^{13}\text{C}$ ). Because catchment vegetation determines POC, carbon stable isotopes provide a powerful tool for detecting shifts in vegetation due to anthropogenic impacts such as deforestation and cultivation, which are often associated with a shift from C3 plants (trees) to C4 dominated communities (grasses, maize). These studies represent an important step in exploring the value of carbon isotopes in examining the impact of land use changes on aquatic systems.

Alone, carbon isotopes are only minimally useful. Carbon isotopes can only distinguish between C3 and C4 plant material, limiting this approach to tropical climatic regimes where C4 plants are found. It is difficult to distinguish between C3 terrestrial plant material and phytoplankton (also C3 plants) using carbon isotopes, and the contribution of algal carbon is either dismissed *a priori* (Bird et al. 1994; Bird et al. 1998) or indirectly estimated (Cai et al. 1988; Martinelli et al. 1999). Studies have used other biochemical indicators, such as lignin phenols, to determine the proportion of terrestrial

plant material (Hedges et al. 2000; Onstad et al. 2000), but these approaches are often time consuming and more expensive.

Combining data from carbon isotopes with other geochemical indicators such as carbon:nitrogen ratios and nitrogen isotopes can provide more information on land use changes. Carbon:nitrogen (C:N) ratios of the organic matter distinguish clearly between terrestrial and aquatic material, with terrestrial plant material having a higher proportion of carbon required for woody support tissues (Meyers 1994). Because changes in vegetation patterns may also be caused by climatic shifts, it is necessary to have an independent indicator of anthropogenic impacts on the watershed. Nitrogen isotopes are useful as indicators of direct human impacts, as nitrogen from soil and human and animal wastes provides an enriched  $\delta^{15}\text{N}$  signal that can be traced within a catchment (Kendall 1998; Kao and Liu 2000).

We evaluated carbon and nitrogen isotopes and the C:N ratio in sedimentary organic matter (SOM) as indicators of land use patterns in the Lake Tanganyika watershed, East Africa. High population growth along the northeast lakeshore has led to rapid deforestation and conversion to open grassland and agriculture. This shifts the landscape from one dominated by C3 trees to one dominated by C4 grasses, which should be clearly evident as an enrichment in the carbon isotope signal. C:N ratios should allow us to distinguish between autochthonous and allochthonous material, with higher ratios in the impacted watersheds indicating a greater proportion of terrestrial plant material. Furthermore, we expect to see differences in the  $\delta^{15}\text{N}$  values of the organic matter, with impacted watersheds having more enriched values indicative of soil or waste nitrogen.

Finally, if these biogeochemical indicators reflect watershed land use patterns, we should be able to detect these anthropogenic changes in the paleolimnological record. We tested this by analyzing cores taken offshore from several impacted or unimpacted watersheds. Stable isotope analyses of the cores should be consistent with patterns seen in the surface sediments. Prior to extensive human settlement in the 1800's we expect the geochemical signatures of the cores to be similar, with a subsequent change to enriched carbon and nitrogen isotopes and higher C:N ratios in the impacted watersheds commensurate with historical records of population demographics.

## **Methods**

### *Study sites*

Lake Tanganyika is a large rift valley lake located in East Africa (Figure A.1), with a catchment that contains many small rivers draining the rift escarpment and a few larger river systems that drain areas behind the escarpment. The lake is permanently stratified, with periodic wind-driven upwelling events that introduce deeper nutrient-rich water to the surface occurring during the dry season. Precipitation in this region is between 820 and 1600 mm yr<sup>-1</sup>, almost all of which falls during the wet season between mid-December and early May (Verburg et al. 1998). Vegetation in unimpacted (or moderately impacted) watersheds consists primarily of semi-deciduous woodland and canopy forests with areas of open grassland at higher elevations. Impacted areas have high population densities and population growth rates as high as 3.15% (CIA 2000). Deforestation rates are as high as 100% in the north and 40% to 60% in the central areas

(Cohen et al. 1993), and cleared land is used for cultivation of bananas, maize, cassava, and other vegetables.

We chose river delta sediments because they provide both spatial and temporal coverage of the entire watershed. Riverine POC composition can be related to discharge and may show large seasonal shifts of up to 6‰  $\delta^{13}\text{C}$  (Bird et al. 1998). At a minimum, this necessitates sampling across seasonal scales in order to accurately characterize POC, and even then, interannual variability may lead to anomalous results. Other work on Lake Tanganyika (Cohen et al. 1999) and dating of the sediment cores allowed us to determine sedimentation rates in the deltas, providing an estimate for the temporal integration of our samples.

### *Surface sediments*

We sampled four river deltas in the lake whose watersheds range in size and in disturbance (Mitumba, Mwamgongo, Luiche, Luegere; Figure A.1; Table A.1). Two of the rivers of these drain small watersheds north of Kigoma, Tanzania. One of these small watersheds (Mitumba) is along the northern boundary within Gombe Stream National Park and is protected. Population densities in this area were reduced after gazettement of the park as a reserve in 1942 and human impacts have remained low. The other small watershed (Mwamgongo) is adjacent to the northern boundary outside the park and is now highly impacted. Although population densities were once probably comparable to those of Mitumba, there was a rapid increase in population size due to relocation after the gazettement of the park. Another major increase in population size occurred in 1972, during

the Tanzanian government's "ujamaa" village program, which relocated rural populations to villages to improve infrastructure and social services. This watershed is almost completely deforested and extensively cultivated.

The other two rivers drain much larger areas and have floodplains near the river mouth that are dominated by grasses and floating macrophytes. The unimpacted watershed (Luegere) is located north of Mahale Mountains National Park. As this area is relatively isolated, human population densities are low and agricultural impacts are minimal. The large impacted watershed (Luiche) drains the land around Kigoma, which is the largest Tanzanian town in this region. Human population densities are high, and added pressure of refugees over the past decade has intensified impacts on the land. In addition to the high anthropogenic impacts throughout the watershed, the floodplain of this river is cultivated during the dry season.

We characterized surface sediments by collecting spatially distributed samples at each river delta. At the two small watersheds, surface sediments were sampled along three transect lines (north, central, and south of the river mouth) at depths of 2, 5, 10, and 20 m using SCUBA. At the two large watersheds, where SCUBA was unsafe due to the potential presence of crocodiles, depth was determined using a plumb line and samples were taken using an Eckman sampler at depths as close to 2, 5, and 10 m as possible. At both large river deltas, a shell lag from a older water low level was encountered beginning around 8 m, and obtaining samples deeper than this was difficult. Approximately the upper 1 cm of sediment was collected, which probably represents

several years to approximately 10 years of deposition based on sedimentation rates obtained from both deepwater and nearshore cores (Alin et al. in prep).

### *Cores*

Stable isotope analyses were also done on cores previously collected along the northeast shoreline (Karonge/Kirasa, Mwamgongo, Nyasanga/Kahama, Mgondozi; Figure A.1.; Table A.1.). Again, we used cores from two unimpacted and two impacted watersheds, although in this case area remained relatively constant among watersheds. One of the cores (Mwamgongo – LT-98-37M) is from a site that was included in the surface sediment portion of this study. Another core (Nyasanga/Kahama – LT-98-58M) is also from Gombe Stream National Park and is from the watershed adjacent to Mitumba, in which the surface samples were collected. The other two core sites are from an unimpacted area near the Luegere watershed (Mgondozi –T97-57V) and a highly impacted watershed in Burundi (Karonge/Kirasa – LT-98-82M). Three cores were collected using a Hedrick-Marrs Multicorer as part of the UNDP/GEF Lake Tanganyika Biodiversity Project and dated using  $^{210}\text{Pb}$  and  $^{14}\text{C}$  (Cohen et al. 1999). The fourth core (Mgondozi) was collected using a vibracore during a cruise in 1997 and dated using  $^{210}\text{Pb}$ . We analyzed organic matter for carbon and nitrogen isotopes approximately every 3 cm, with the exception of the top 3 to 6 cm, for which there was not enough material remaining after earlier work on these cores. As Mwamgongo and Karonge/Kirasa have historically undergone land use change as populations have increased, we expected to see this change represented as a shift in the core isotopic ratios.

Since 1840, there has been a significant atmospheric depletion of 1.4‰  $\delta^{13}\text{C}_{\text{atm}}$  due to fossil fuel burning (the Suess effect) (Keeling et al. 1989). We corrected for this historic depletion using fossil air trapped in ice cores (Friedli et al. 1986) to develop the regression function ( $r^2=0.67$ ,  $p<0.0004$ ):

$$\delta^{13}\text{C}_{\text{atm}} = 1.53 \times 10^{-7} t^3 - 1 \times 10^{-5} t^2 - 0.00339 t - 6.7421$$

where  $t$  is the time (years) since 1840. The difference in  $^{13}\text{C}$  between this time-dependent value and the 1840's value was added to the measured  $\delta^{13}\text{C}_{\text{org}}$  for the dated sediment sections.

All core and sediment samples were acidified with 10% HCl for at least 24 hours and rinsed three times by decanting after centrifugation. Bulk sedimentary organic matter was analyzed at the University of Waterloo Environmental Isotope Lab on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1108) with standard error of 0.2‰ for carbon and 0.3‰ for nitrogen. Samples with low %N were run additionally at the University of Arizona on a recently acquired Finnigan Delta-plus Continuous Flow Mass Spectrometer coupled to a Costech Elemental Analyzer with a standard error of 0.05‰ for carbon and 0.15‰ for nitrogen. The isotope ratios are expressed in delta notation with respect to deviations from standard reference material (Pee Dee belemnite carbon and atmospheric nitrogen). Statistical analyses were done using JMP IN (SAS Institute, Inc., 1999).

## Results

### *Surface sediments*

SOM carbon and nitrogen isotopic ratios and C:N ratios were significantly related to watershed size and disturbance (Figures A.2., Table A.2.). Carbon isotopes were significantly enriched at larger sites (ANOVA,  $F=45.1$ ,  $p<.0001$ ) but not disturbed sites (ANOVA,  $F=0.6$ ,  $p=.44$ ). Nitrogen was significantly enriched at disturbed sites (ANOVA,  $F=25.1$ ,  $p<.0001$ ) and at smaller sites (ANOVA,  $F=12.2$ ,  $p=.0012$ ), with a significant interaction between size and disturbance (ANOVA,  $F=136.4$ ,  $p<.0001$ ). For the small unimpacted watershed, the river sample and one 2 m sample also showed enriched nitrogen values. The C:N ratio increased significantly with both size (ANOVA,  $F=3.7$ ,  $p=.06$ ) and disturbance (ANOVA,  $F=4.2$ ,  $p=.05$ ), with a significant interaction between size and disturbance (ANOVA,  $F=45.6$ ,  $p<.0001$ ).

Larger watersheds had significantly more organic carbon than smaller watersheds (ANOVA,  $F=22.1$ ,  $p<.0001$ ), but there was no relationship with land use. Carbon isotopes became significantly enriched as C:N ratios increased ( $r^2=0.62$ ,  $p<.0001$ ), but there was no significant relationship between  $\delta^{15}\text{N}$  and C:N. Samples became depleted in  $\delta^{13}\text{C}$  with depth (ANOVA,  $F=5.4$ ,  $p=.03$ ) for the larger watersheds. The upriver samples did not differ significantly from those in the delta systems.

### *Cores*

The unimpacted cores were similar in many respects (Figure A.5., Table A.3.). Corrected  $^{13}\text{C}$  isotopes were slightly enriched at Mgondozi, but both cores showed a

general trend towards depleted  $\delta^{13}\text{C}$  values. Nitrogen isotopes remained relatively constant at Mgondozi, while Nyasanga had a period of enriched  $^{15}\text{N}$  beginning after 1800, with some values becoming depleted and similar to Mgondozi near the upper sections of the core. C:N ratios were similar between the cores and did not change significantly throughout this time period.

The impacted cores showed different isotopic patterns compared to the unimpacted cores, particularly with respect to nitrogen isotopes (Figure A.6., Table A.3.). Kironge/Kirasa showed an initial enrichment in  $\delta^{13}\text{C}$ , but both cores had a depletion in carbon isotopes in the upper sections. Both cores had more enriched  $\delta^{15}\text{N}$  than the unimpacted cores throughout and showed a general pattern of  $^{15}\text{N}$  enrichment over time, with the initial shift beginning in 1845 at Kironge/Kirasa and in the 1920's at Mwamgongo. Although they were higher at Mwamgongo, C:N ratios did not change much throughout either impacted core; however, the C:N ratios were lower than those of the unimpacted watersheds.

## **Discussion**

### *Surface sediments*

Each river delta appears to have its own unique signature with respect to carbon and nitrogen isotopes (Figure A.2A.) and C:N ratios (Figure A.2B and A.2C). This suggests that land use patterns and/or watershed size might have an important role in determining terrestrial inputs to the lake. However, closer analysis shows that this pattern is not as straightforward as it might be expected.

The small protected watershed (Mitumba) has a geochemical signature consistent with its land use pattern. The depleted  $\delta^{15}\text{N}$  values are consistent with an unimpacted watershed. The depleted carbon isotopes suggest C3 plant material and low C:N ratios further imply that this organic matter is derived from autochthonous material. The samples with enriched  $\delta^{15}\text{N}$  and higher C:N are from the river mouth and in shallow water (Table A.2.), and may be due to input of terrestrial soil and C3 plant material such as leaves. The river mouth of this stream has the most anthropogenic impact, as the staff office for Gombe Stream National Park are located nearby. Clearly, however, any impact is relatively low, as its signal is limited to only a few locations on the river delta.

Similarly, the small highly-impacted watershed (Mwamgongo) is consistent with its expected geochemical signature. Nitrogen isotopes are enriched, suggesting the input of soil nitrogen (Kendall 1998; Kao and Liu 2000). Although the carbon isotopes are similar to that of the unimpacted watershed, the higher C:N ratios suggest that this organic matter contains a significant proportion of terrestrial material (Figure A.2C.).

The large, unimpacted watershed (Luegere) also has a sedimentary signal that can be explained by a combination of vegetation and land use patterns. The  $\delta^{15}\text{N}$  values lie between those of the protected and impacted watersheds described above, consistent with low to moderate anthropogenic activity. Carbon isotopes span a range of values from those similar to the small watershed to more enriched values, and C:N ratios tend to be high. This suggests that the sedimentary organic carbon is composed in part of C4 plant material which may derive from the wetland grasses growing on the floodplain.

The large impacted watershed (Luiche) does not fit the pattern established by the other watersheds. Although the enriched  $\delta^{13}\text{C}$  values suggest terrestrial C4 plant inputs, C:N ratios are low, indicating dominance by autochthonous material.  $\delta^{15}\text{N}$  values are depleted in spite of heavy anthropogenic impact (Figure A.2C.). Here, intense land use may have crossed a threshold level after which effects on the aquatic environment are dramatically different. At this intensity, land use has increased nutrient inputs to the lake with higher algal productivity rates, causing enriched  $\delta^{13}\text{C}$  values (Farquhar et al. 1989). Soil erosion often leads to high inputs of phosphorus (Schlesinger 1997), creating a nitrogen-limited system that would promote cyanobacterial growth. Cyanobacteria are capable of nitrogen fixation and have an  $\delta^{15}\text{N}$  signal near 0 – 1‰, reflecting their atmospheric N source (Hecky and Hesslein 1995). This explanation fulfills the requirements for low C:N, enriched  $\delta^{13}\text{C}$ , and depleted  $\delta^{15}\text{N}$ .

For three of the watersheds, geochemical signal reflected vegetation and land use patterns. Nitrogen isotopes were correlated to land use patterns, probably because increased erosion and inputs of relatively enriched soil nitrogen. C:N isoptes were also related to land use patterns in that they were useful in distinguishing between autochthonous and allochthonous carbon sources. Carbon isotopic variation can be attributed to watershed vegetation patterns. These results are consistent with carbon isotopic studies of riverine POC and sediments (Bird et al. 1994; Bird et al. 1998; Martinelli et al. 1999) and suggest these river delta sediments do reflect watershed vegetation patterns. The large, highly impacted watershed is distinguished by processes

that are related to land use change (nutrient inputs) but have a very different influence on the sedimentary organic matter signature because terrestrial nutrient inputs may have caused increased autochthonous productivity.

### *Cores*

As with the surface sediments, nitrogen isotopes appear to track land use changes. The impacted cores have more enriched  $\delta^{15}\text{N}$  values than the unimpacted cores. However, these enrichments begin prior to historical records of sudden increases in population densities in these watersheds. For example, the Mwamgongo watershed shows  $^{15}\text{N}$  enrichment around 1920, while historical records indicate that the major increases in population occurred during independence and with the formation of Gombe Stream National Park, both in the 1960s. These enrichments may still indicate land use changes associated with anthropogenic impacts. Paleolimnological studies on other lakes have detected soil erosion and deforestation several thousands of years before archaeological evidence shows high population densities (Curtis et al. 1998). Since these rivers drain a steeply sloping rift valley escarpment, small changes in land use may easily cause extensive soil erosion. The changes in the Nyasanga core may also relate to anthropogenic disturbance, as this enrichment in  $^{15}\text{N}$  occurs prior to the formation of the National Park.

Carbon isotopic ratios in the cores do not correlate with land use patterns and appear to be reflecting autochthonous processes. The dominance of autochthonous carbon in the cores compared to the surface sediments may be due in part to the depth and distance

from shore of the cores. Carbon isotopes show a general (post-1900) trend towards depleted values, even at closely located watersheds with different land use patterns (i.e. Mwangongo vs. Nyasanga). Within an aquatic environment, a depletion in  $\delta^{13}\text{C}$  values often indicates a lake-wide decrease in productivity. The lake is permanently stratified, and periodic upwelling of deeper waters provides an important source of nutrients (O'Reilly et al. in press). Global warming may have increased the thermal stability of the lake, reducing the frequency or intensity of upwelling events and causing a decrease in productivity.

Unlike for the surface sediments, the C:N ratios do not provide useful information on the carbon source. Instead, the C:N ratios are inconsistent with our predictions as the unimpacted cores have higher C:N ratios than the impacted ones. This may be due to better preservation of organic matter at the impacted sites, as these cores were taken at 95 m, which is near the average oxycline (100m) at this location in the lake (Coulter and Spigel 1991), increasing the likelihood of anoxia and good conditions for preservation. The cores from the unimpacted sites were taken in shallower water at 76 m, and conditions for preservation may be less optimal at this depth. Alternatively, the lower C:N ratios at the deeper cores could reflect a higher relative proportion of autochthonous material because allochthonous matter settles out of the water column at shallower depths near the shoreline of the lake. This is consistent with the fact that the surface sediments, which were collected at much shallower water depths, had stronger signals related to their land use patterns than the cores.

In general, diagenesis is unlikely to be a major problem in geochemical record of these sediments. Although selective degradation of organic matter can affect C:N ratios, with older OM often having lower values than more recent OM, these changes are not enough to erase the difference in C:N between vascular and non-vascular plants (Meyers and Ishiwatari 1993). While diagenesis of isotopic composition may occur in sediments with high %OC (> 20 to 28%) (Meyers and Ishiwatari 1993), these surface sediments and cores all have carbon concentrations of less than 20% (Table A.2. and A.3.).

### **Conclusion**

This study suggests that the combined information from carbon and nitrogen isotopes and C:N ratios in river delta SOM can provide information about vegetation and land use patterns. River deltas were an effective location for sampling watershed scale processes and provided information that was integrated across seasonal time periods and over the spatial extent of the catchment. Carbon isotopes generally reflected watershed vegetation patterns, and C:N ratios allowed us to distinguish between allochthonous and autochthonous material when carbon isotopes were inconclusive. Nitrogen isotopes provided an indicator of human impacts, and suggested the input of soil nitrogen at the disturbed sites. However, for each watershed, all three geochemical signals were required to determine the most plausible interpretation. Changes in land use patterns were detected in the sedimentary records of the watersheds, and these changes corresponded with historical records of population demographics.

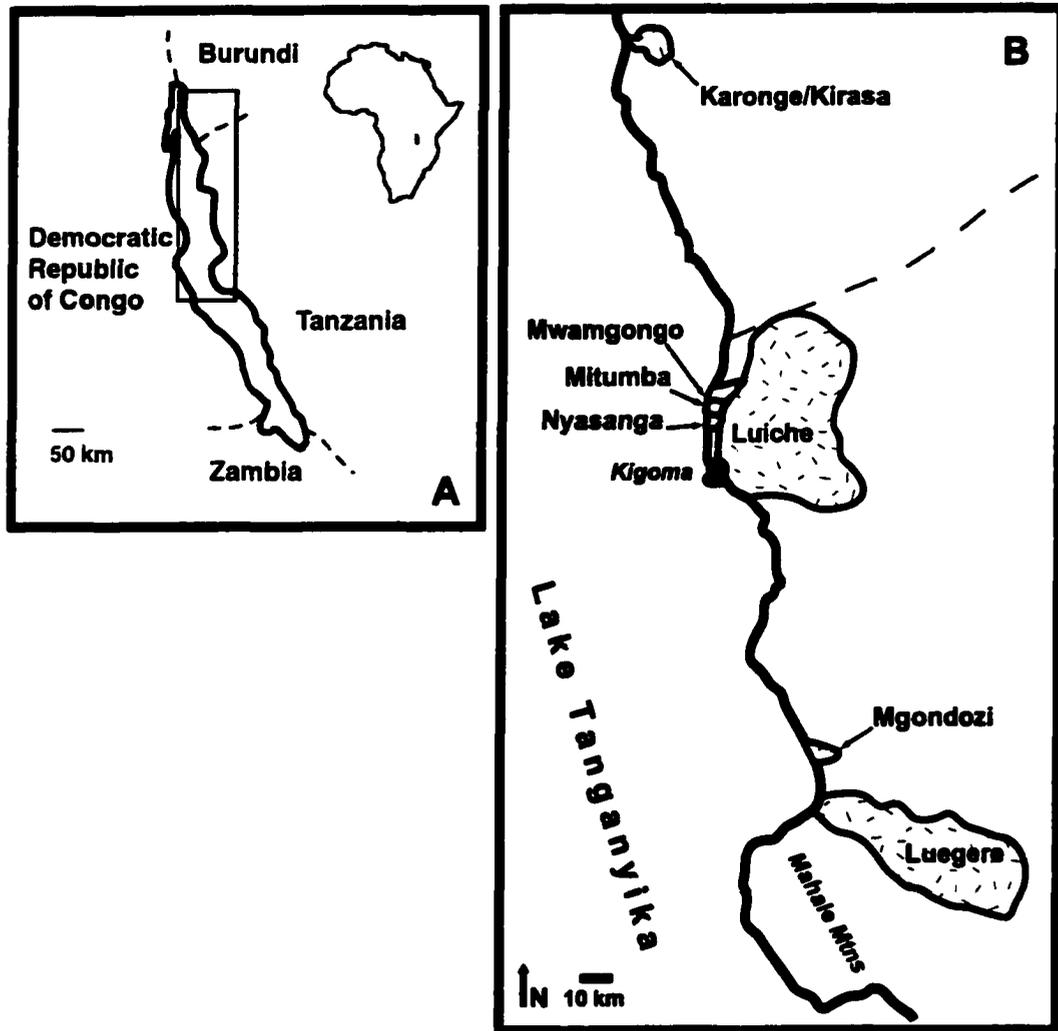


Figure A.1. A – The location of Lake Tanganyika in East Africa. The shaded box represents that area in which our sampling took place and is shown in more detail in B. B – Location of the study sites. Further details of the watersheds are given in Table A.1.

**Table A. 1. Details of the watersheds and cores. High impact sites are associated with near-100% deforestation, while moderately impacted sites may have up to 20% deforestation and some naturally occurring open grassland. The protected sites have less than 10% open grassland and lie within Gombe Stream National Park.**

| <b>Watershed</b>        | <b>Human impact and history</b>                             | <b>Watershed area (km<sup>2</sup>)</b> | <b>Population density (PD) (people/km<sup>2</sup>) (1988 or 1990)</b> | <b>sample type</b>       | <b>core depth (m)</b> | <b>distance from shore (m)</b> |
|-------------------------|---|--|---|--------------------------|-----------------------|--------------------------------|
| <b>Mitumba</b>          | <b>protected/<br/>brief period of moderate PD</b>           | <b>2.5</b>                             | <b>&lt;5</b>  | <b>surface</b>           |                       |                                |
| <b>Nyasanga/ Kahama</b> | <b>protected/<br/>brief period of moderate PD</b>           | <b>2</b>                               | <b>&lt;5</b>  | <b>core</b>              | <b>76</b>             | <b>300</b>                     |
| <b>Mwamgongo</b>        | <b>high/<br/>dramatic increase in PD since 1960's</b>       | <b>8</b>                               | <b>580</b>  | <b>core,<br/>surface</b> | <b>95</b>             | <b>300</b>                     |
| <b>Luegere</b>          | <b>moderate/<br/>moderate increase in PD</b>                | <b>1337</b>                            | <b>17</b>   | <b>surface</b>           |                       |                                |
| <b>Luiche</b>           | <b>high/<br/>high increase in PD</b>                        | <b>1880</b>                            | <b>38<br/>(50 to 600)</b>   | <b>surface</b>           |                       |                                |
| <b>Mgondozi</b>         | <b>moderate/<br/>moderate increase in PD</b>                | <b>5.7</b>                             | <b>17</b>   | <b>core</b>              | <b>76</b>             | <b>1500</b>                    |
| <b>Karonge/Kirasa</b>   | <b>high/<br/>dramatic increase in PD since early 1900's</b> | <b>162</b>                             | <b>475</b>  | <b>core</b>              | <b>96</b>             | <b>1200</b>                    |

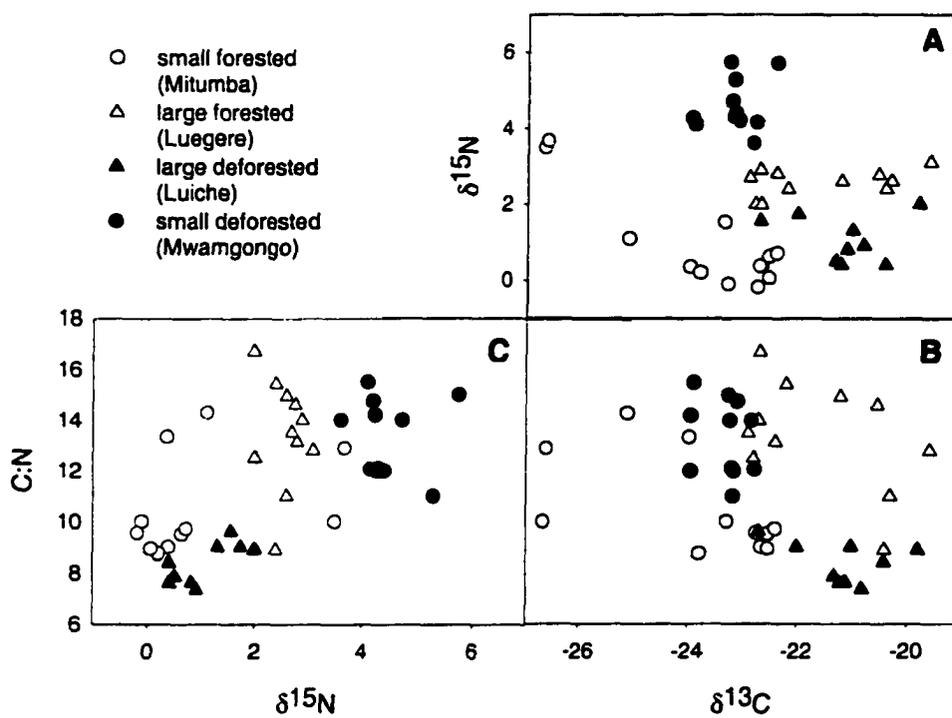


Figure A.2. Geochemistry of the surface SOM, showing C:N ratios,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$ .

Table A. 2. Surface sediment geochemistry

|         | transect * | depth (m) | $\delta^{13}C$ | $\delta^{15}N$ | %C    | %N    | C:N   |
|---------|------------|-----------|----------------|----------------|-------|-------|-------|
| Mitumba | R          | 1         | -26.67         | 3.50           | 0.100 | 0.010 | 10.00 |
|         | N          | 20        | -25.10         | 1.10           | 0.200 | 0.014 | 14.29 |
|         | N          | 10        | -22.75         | -0.18          | 0.277 | 0.029 | 9.55  |
|         | N          | 5         | -23.36         | 1.53           | n/a   | n/a   | n/a   |
|         | N          | 2         | -22.71         | 0.37           | n/a   | n/a   | n/a   |
|         | C          | 20        | -23.30         | -0.10          | 0.070 | 0.007 | 10.00 |
|         | C          | 5         | -22.66         | 0.38           | 0.090 | 0.010 | 9.00  |
|         | C          | 2         | -22.54         | 0.62           | 0.190 | 0.020 | 9.50  |
|         | C          | 10        | -23.98         | 0.35           | 0.400 | 0.030 | 13.33 |
|         | S          | 2         | -26.62         | 3.67           | 0.632 | 0.049 | 12.90 |
|         | S          | 10        | -23.80         | 0.20           | 0.070 | 0.008 | 8.75  |
|         | S          | 20        | -22.40         | 0.70           | 0.068 | 0.007 | 9.71  |
|         | S          | 5         | -22.54         | 0.06           | 0.161 | 0.018 | 8.94  |
|         | Mwamgongo  | R         | 1              | -22.40         | 5.70  | 0.139 | 0.015 |
| N       |            | 10        | -23.10         | 4.20           | 0.118 | 0.008 | 14.75 |
| N       |            | 20        | -23.90         | 4.10           | 0.186 | 0.012 | 15.50 |
| N       |            | 5         | -23.95         | 4.28           | 0.480 | 0.040 | 12.00 |
| N       |            | 2         | -23.24         | 4.72           | 0.280 | 0.020 | 14.00 |
| C       |            | 5         | -23.20         | 4.30           | 0.121 | 0.010 | 12.10 |
| C       |            | 20        | -23.95         | 4.24           | 0.681 | 0.048 | 14.19 |
| C       |            | 5         | -23.19         | 5.28           | 0.440 | 0.040 | 11.00 |
| C       |            | 2         | -23.17         | 4.40           | 0.360 | 0.030 | 12.00 |
| S       |            | 10        | -22.84         | 3.61           | 0.322 | 0.023 | 14.00 |
| S       |            | 20        | -22.78         | 4.15           | 0.193 | 0.016 | 12.06 |
| S       |            | 5         | -23.27         | 5.74           | 0.150 | 0.010 | 15.00 |
| Luegere |            | R         | 1              | -22.90         | 2.70  | 0.270 | 0.020 |
|         | N          | 8         | -22.20         | 2.40           | 0.324 | 0.021 | 15.43 |
|         | N          | 2         | -20.30         | 2.60           | 0.055 | 0.005 | 11.00 |

|                |        |      |        |        |       |       |       |
|----------------|--------|------|--------|--------|-------|-------|-------|
| Luegere, cont. | N      | 7.3  | -22.69 | 1.98   | 0.018 | 0.001 | 16.70 |
|                | C      | 4    | -22.80 | 2.00   | 0.050 | 0.004 | 12.50 |
|                | C      | 6.4  | -22.70 | 2.90   | 0.378 | 0.027 | 14.00 |
|                | C      | 8.5  | -22.40 | 2.80   | 0.184 | 0.014 | 13.14 |
|                | C      | 1.75 | -20.53 | 2.77   | 0.219 | 0.015 | 14.60 |
|                | S      | 8    | -21.20 | 2.60   | 0.254 | 0.017 | 14.94 |
|                | S      | 2.2  | -19.60 | 3.10   | 0.055 | 0.005 | 12.80 |
|                | S      | 4.75 | -20.40 | 2.40   | 0.435 | 0.031 | 8.89  |
|                | Luiche | R    | 1      | -23.10 | 2.70  | 0.398 | 0.032 |
| R              |        | 2    | -21.40 | 4.10   | 0.417 | 0.031 | 13.45 |
| N              |        | 4    | -21.20 | 0.40   | 0.213 | 0.028 | 7.61  |
| N              |        | 2.3  | -21.10 | 0.80   | 0.145 | 0.019 | 7.63  |
| N              |        | 15   | -19.80 | 2.00   | 0.320 | 0.036 | 8.89  |
| C              |        | 2    | -22.00 | 1.73   | 0.080 | 0.009 | 9.00  |
| C              |        | 4    | -21.30 | 0.50   | 0.110 | 0.014 | 7.86  |
| C              |        | 5.5  | -20.40 | 0.40   | 0.210 | 0.025 | 8.40  |
| S              |        | 1.5  | -22.70 | 1.56   | 0.048 | 0.005 | 9.60  |
| S              |        | 4.5  | -21.00 | 1.30   | 0.108 | 0.012 | 9.00  |
| S              |        | 6.5  | -20.80 | 0.90   | 0.191 | 0.026 | 7.35  |

\* N = north of river mouth, C = central off river mouth, S = south of river mouth, R = upstream from river mouth.

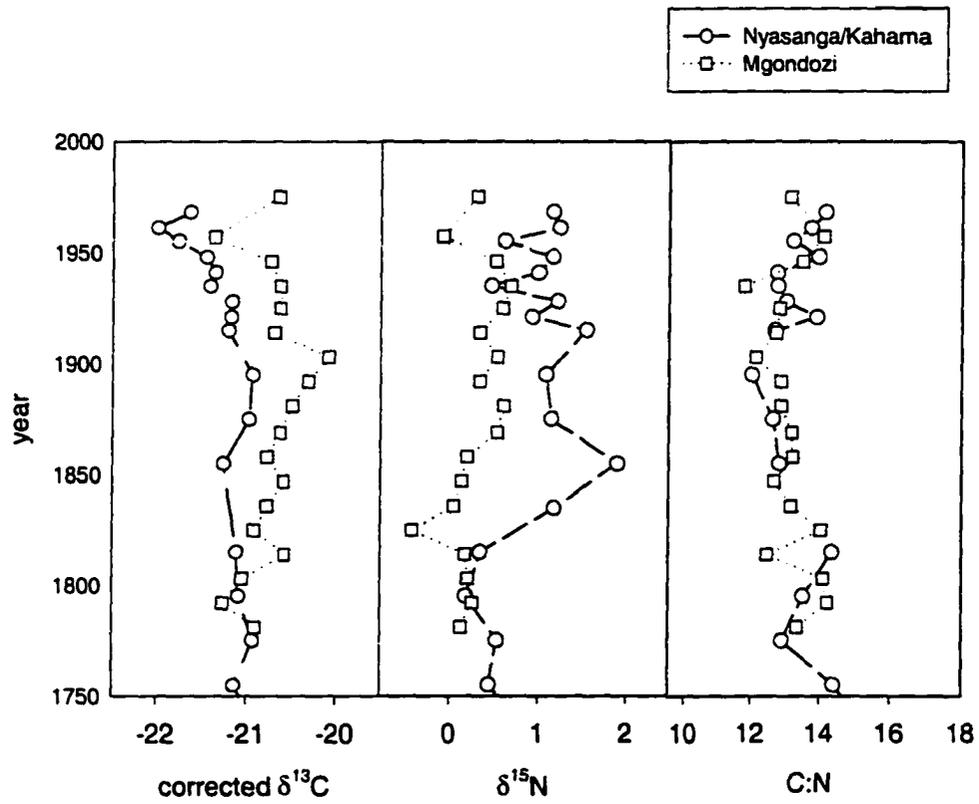


Figure A.3. Stable isotope composition of organic matter in cores from unimpacted watersheds. Corrected  $\delta^{13}\text{C}$  values were calculated to account for the Suess effect (see text).

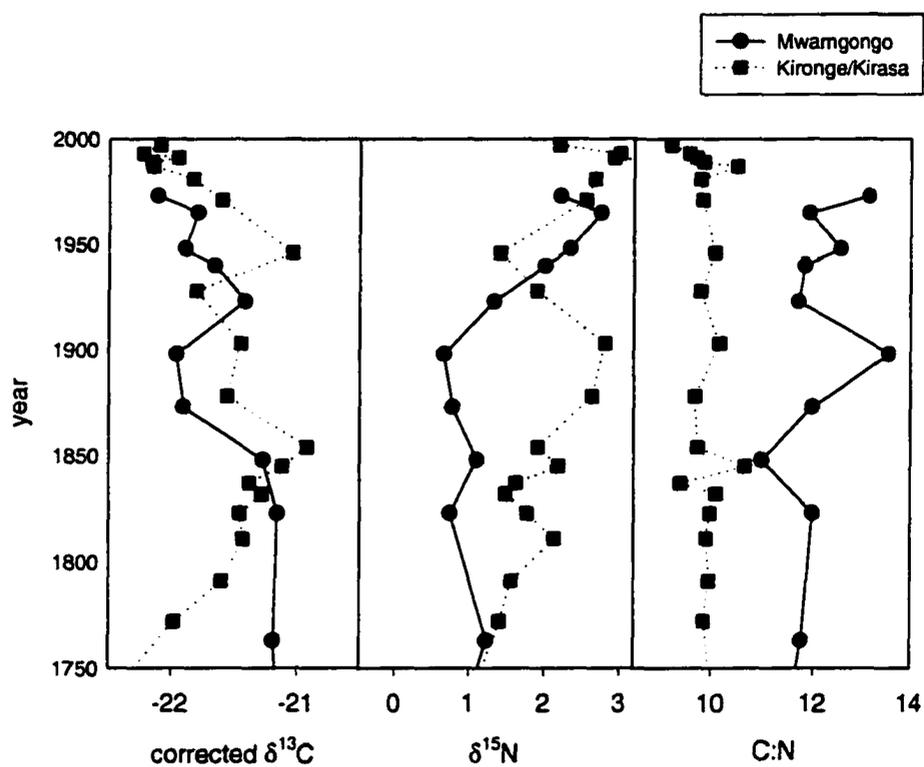


Figure A.4. Stable isotope composition of organic matter in cores from impacted watersheds. Corrected  $\delta^{13}\text{C}$  values were calculated to account for the Suess effect (see text). Note difference in x-axis scales between this figure and Figure A.5.

Table A.3. Core geochemistry

|                              | depth (cm) | age    | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | %C    | %N    | C:N   |
|------------------------------|------------|--------|-----------------------|-----------------------|-------|-------|-------|
| Nyasanga/Kahama<br>LT-98-58M | 4.5        | 1968   | -22.18                | 1.16                  | 2.335 | 0.165 | 14.15 |
|                              | 5.5        | 1961   | -22.55                | 1.24                  | 3.438 | 0.25  | 13.75 |
|                              | 6.5        | 1955   | -22.32                | 0.62                  | 3.711 | 0.281 | 13.21 |
|                              | 7.5        | 1948   | -22.01                | 1.16                  | 2.918 | 0.209 | 13.96 |
|                              | 8.5        | 1941   | -21.91                | 1.00                  | 2.703 | 0.212 | 12.75 |
|                              | 9.5        | 1935   | -21.96                | 0.47                  | 3.272 | 0.256 | 12.78 |
|                              | 10.5       | 1928   | -21.71                | 1.22                  | 2.317 | 0.178 | 13.02 |
|                              | 11.5       | 1921   | -21.71                | 0.93                  | 1.863 | 0.134 | 13.90 |
|                              | 12.5       | 1915   | -21.72                | 1.54                  | 1.586 | 0.125 | 12.69 |
|                              | 13.5       | 1908   | -22.53                | 1.08                  | 2.195 | 0.142 | 15.46 |
|                              | 15.5       | 1895   | -21.40                | 1.09                  | 1.442 | 0.12  | 12.02 |
|                              | 18.5       | 1875   | -21.37                | 1.15                  | 2.338 | 0.185 | 12.64 |
|                              | 21.5       | 1855   | -21.58                | 1.89                  | 2.294 | 0.179 | 12.82 |
|                              | 24.5       | 1835   | -74.75                | 1.18                  | 2.593 | 0.252 | 10.29 |
|                              | 27.5       | 1815   | -21.11                | 0.35                  | 2.871 | 0.2   | 14.36 |
|                              | 30.5       | 1795   | -21.09                | 0.19                  | 2.92  | 0.216 | 13.52 |
| 33.5                         | 1775       | -20.93 | 0.54                  | 3.972                 | 0.308 | 12.90 |       |
| 36.5                         | 1755       | -21.14 | 0.45                  | 3.099                 | 0.215 | 14.41 |       |
| 37.5                         | 1748       | -21.04 | 0.60                  | 2.586                 | 0.175 | 14.78 |       |
| Mwamgongo<br>LT-98-37M       | 3.5        | 1969   | -22.66                | 2.21                  | 3.177 | 0.242 | 13.13 |
|                              | 4.5        | 1961   | -22.35                | 2.75                  | 2.787 | 0.234 | 11.91 |
|                              | 6.5        | 1944   | -22.45                | 2.34                  | 3.724 | 0.297 | 12.54 |
|                              | 8.5        | 1927   | -22.20                | 2.01                  | 3.855 | 0.326 | 11.83 |
|                              | 9.5        | 1919   | -21.94                | 1.33                  | 4.199 | 0.359 | 11.70 |
|                              | 12.5       | 1894   | -22.42                | 0.66                  | 4.038 | 0.298 | 13.55 |
|                              | 15.5       | 1869   | -22.28                | 0.77                  | 4.872 | 0.407 | 11.97 |
|                              | 18.5       | 1844   | -21.56                | 1.10                  | 5.156 | 0.47  | 10.97 |
| 21.5                         | 1819       | -21.16 | 0.74                  | 3.33                  | 0.278 | 11.98 |       |

|                                   |      |        |        |       |       |       |       |
|-----------------------------------|------|--------|--------|-------|-------|-------|-------|
| <b>Mwamgongo,<br/>cont.</b>       | 24.5 | 1794   | -21.19 | 1.23  | 2.858 | 0.243 | 11.76 |
|                                   | 27.5 | 1769   | -21.13 | 0.71  | 4.235 | 0.374 | 11.32 |
|                                   | 30.5 | 1744   | -21.09 | 0.43  | 5.329 | 0.457 | 11.66 |
|                                   | 33.5 | 1719   | -21.13 | 0.55  | 5.584 | 0.491 | 11.37 |
|                                   | 36.5 | 1694   | -21.11 | 0.44  | 5.383 | 0.454 | 11.86 |
|                                   | 39.5 | 1669   | -21.19 | -0.52 | 1.937 | 0.136 | 14.24 |
|                                   | 42.5 | 1644   | -20.96 | 0.41  | 5.358 | 0.446 | 12.01 |
|                                   | 43.5 | 1636   | -20.96 | 0.54  | 5.066 | 0.448 | 11.31 |
| <b>Mgondozi<br/>LT-98-82M</b>     | 2.5  | 1975   | -21.18 | 0.31  | 3.31  | 0.25  | 13.14 |
|                                   | 4.5  | 1957   | -21.92 | -0.08 | 3.40  | 0.24  | 14.10 |
|                                   | 6.5  | 1946   | -21.30 | 0.52  | 3.20  | 0.24  | 13.49 |
|                                   | 8.5  | 1935   | -21.18 | 0.69  | 3.15  | 0.27  | 11.79 |
|                                   | 10.5 | 1925   | -21.17 | 0.60  | 3.18  | 0.25  | 12.83 |
|                                   | 12.5 | 1914   | -21.22 | 0.34  | 3.39  | 0.27  | 12.73 |
|                                   | 14.5 | 1903   | -20.56 | 0.54  | 3.07  | 0.25  | 12.13 |
|                                   | 16.5 | 1892   | -20.76 | 0.34  | 3.45  | 0.27  | 12.86 |
|                                   | 18.5 | 1881   | -20.90 | 0.61  | 3.40  | 0.26  | 12.87 |
|                                   | 20.5 | 1869   | -21.01 | 0.54  | 3.35  | 0.25  | 13.19 |
|                                   | 22.5 | 1858   | -21.12 | 0.20  | 3.33  | 0.25  | 13.21 |
|                                   | 24.5 | 1847   | -20.88 | 0.14  | 3.21  | 0.25  | 12.68 |
|                                   | 26.5 | 1836   | -20.78 | 0.05  | 3.04  | 0.23  | 13.16 |
|                                   | 28.5 | 1825   | -20.92 | -0.42 | 1.59  | 0.11  | 14.04 |
|                                   | 30.5 | 1814   | -20.58 | 0.18  | 3.03  | 0.24  | 12.47 |
|                                   | 32.5 | 1803   | -21.05 | 0.21  | 2.45  | 0.17  | 14.10 |
| 34.5                              | 1792 | -21.26 | 0.26   | 3.00  | 0.21  | 14.22 |       |
| 36.5                              | 1781 | -20.91 | 0.13   | 2.95  | 0.22  | 13.35 |       |
| <b>Karonge/Kirasa<br/>T97-57V</b> | 2.5  | 1997   | -22.55 | 2.19  | 2.581 | 0.28  | 9.22  |
|                                   | 4.5  | 1993   | -22.71 | 3.00  | 2.726 | 0.285 | 9.56  |
|                                   | 6.5  | 1991   | -22.43 | 2.92  | 2.067 | 0.213 | 9.70  |
|                                   | 8.5  | 1989   | -22.65 | 3.62  | 2.52  | 0.256 | 9.84  |
|                                   | 10.5 | 1987   | -22.65 | 0.34  | 1.007 | 0.096 | 10.49 |

|                          |      |        |        |       |       |       |       |
|--------------------------|------|--------|--------|-------|-------|-------|-------|
| Karonge/Kirasa,<br>cont. | 12.5 | 1981   | -22.36 | 2.67  | 3.027 | 0.309 | 9.80  |
|                          | 14.5 | 1971   | -22.15 | 2.55  | 2.959 | 0.301 | 9.83  |
|                          | 16.5 | 1946   | -21.60 | 1.41  | 2.075 | 0.206 | 10.07 |
|                          | 18.5 | 1928   | -22.35 | 1.90  | 2.889 | 0.295 | 9.79  |
|                          | 20.5 | 1903   | -21.94 | 2.80  | 2.599 | 0.256 | 10.15 |
|                          | 22.5 | 1878   | -21.97 | 2.63  | 3.011 | 0.311 | 9.68  |
|                          | 24.5 | 1854   | -21.25 | 1.91  | 2.463 | 0.253 | 9.74  |
|                          | 26.5 | 1845   | -21.42 | 2.18  | 3.152 | 0.296 | 10.65 |
|                          | 28.5 | 1837   | -21.38 | 1.62  | 3.434 | 0.365 | 9.41  |
|                          | 30.5 | 1832   | -21.28 | 1.48  | 3.168 | 0.314 | 10.09 |
|                          | 32.5 | 1823   | -21.46 | 1.77  | 3.659 | 0.367 | 9.97  |
|                          | 34.5 | 1811   | -21.43 | 2.13  | 3.071 | 0.31  | 9.91  |
|                          | 36.5 | 1791   | -21.60 | 1.56  | 4.36  | 0.438 | 9.95  |
|                          | 38.5 | 1772   | -21.98 | 1.40  | 4.269 | 0.433 | 9.86  |
|                          | 42.5 | 1732   | -22.56 | 1.01  | 4.168 | 0.415 | 10.04 |
| 44.5                     | 1722 | -21.44 | 1.46   | 3.356 | 0.328 | 10.23 |       |

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**APPENDIX B: BENTHIC ALGAL PRODUCTIVITY IN LAKE TANGANYIKA  
AND THE EFFECTS OF DEFORESTATION.**

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## **EXECUTIVE SUMMARY**

This project was designed to collect baseline data on benthic algal productivity in Lake Tanganyika and to determine with increased sediment input is affecting benthic algal dynamics. This work was approached with the following goals:

1. To examine seasonal variation in benthic primary productivity.
2. To examine to effect of upwelling on benthic primary productivity.
3. To compare the following in impacted and forested watersheds:
  - net primary productivity
  - respiration
  - algal biomass
  - light availability
  - amount of inorganic material settled on rock surface

The results of this project are as follows:

- Benthic net productivity does not differ significantly between the forested and deforested watershed.
- Benthic respiration is significantly higher at the impacted watershed.
- There are significantly greater amounts of inorganic material on the rocks at the impacted site.
- Algal biomass is significantly higher at the impacted site.
- There is significantly less oxygen in the water at the impacted site.
- Seasonal variation in net productivity and respiration is not significant in the Kigoma area sites.
- Seasonal variation in net productivity, respiration, and biomass is significant at the Mpulungu site.

## **CHAPTER 1 INTRODUCTION**

Ultimately, lake productivity is dependent on primary producers in the aquatic ecosystem. While planktonic productivity is considered to provide most of the fixed carbon to upper trophic levels in Lake Tanganyika, benthic algae may be an important component of the lake. Most of the biodiversity in this lake is contained within the littoral zone and is supported by a complex food web that may rely heavily on benthic productivity. To date, very little is known about benthic algal productivity in Lake Tanganyika or the potential impacts of land use changes on this important food source.

Lake Tanganyika is a large (mean width 50 km; length 650 km; mean and maximum depths 570 m and 1470 m), oligotrophic, and permanently stratified lake located a few degrees south of the equator (Coulter and Spigel 1991). The clarity of the water allows for light penetration up to 30 m (Hecky et al. 1991), creating a relatively deep littoral area and a large amount of habitat available for colonization by periphyton. A preliminary study at the lake's northern end suggested that periphyton contribute substantially to littoral zone productivity and play an important role in the littoral food web (Takamura 1988). The littoral zone of Lake Tanganyika contains one of the world's most diverse freshwater faunas, and this diversity has been attributed in part to food partitioning of this periphyton resource (Bootsma et al. 1996).

A monsoonal climate creates a large seasonal hydrodynamic pattern in the lake. During the dry-windy season from May to August, strong southerly winds tilt the permanent thermocline and cause upwelling of the deeper nutrient-rich waters at the south end of the lake. Increased nutrient availability from these upwelling events produces phytoplankton blooms that can dramatically reduce water clarity (Plisnier et al. 1999). These changes impact upper trophic levels at the southern end of the lake and are reflected as seasonal patterns in community dynamics among pelagic fish species (Phiri and Shirakihara 1999).

This seasonal pattern in nutrient availability may also have implications for periphyton growth.

Deforestation is increasing throughout the Lake Tanganyika catchment. Erosion rates are as high as 28 to 100 metric tons per year (Bizimana and Duchafour 1991) in intensively cultivated areas in the northern area of the watershed. Increased erosion and sediment input into the lake may have many negative consequences for lake dynamics. Increased sediments can lead to habitat loss, changes in nutrient dynamics, and changes in food quantity and quality for upper trophic levels. The negative effects of increased sedimentation on biodiversity in the lake have already been noted by other researchers (Cohen et al. 1993; Alin et al. 1999), and the impacts are likely to have a greater impact on the littoral zone flora and fauna.

This project had two main goals:

1. To collect baseline information on benthic productivity in Lake Tanganyika, including seasonal variation.
2. To determine whether deforestation is affecting benthic algal productivity.

This report provides data on epilithic productivity for southern Lake Tanganyika and on epilithic and epipelagic productivity for the northern Tanzanian shoreline. The data covers both the wet and dry season, which is particularly important for the southern end of the lake, where seasonal upwelling may affect algal dynamics. By determining the magnitude of benthic productivity and the effects of increased sediment input, this study aimed to quantify the impact of deforestation and to provide some insight to littoral zone dynamics.

## CHAPTER 2 METHODS

### 2.1 Study sites

Four study sites were used throughout the year (Figure 1).

#### *2.1.1 Benthic productivity and seasonal variation*

Jakobsen's Beach (JAK), south of Kigoma, Tanzania was used to do some preliminary work and to establish the methodology. The watershed area is small and human impacts are relatively minor. The lake bottom contained both sandy and rocky substrate.

Mbita Island (MPU), directly north of the port in Mpulungu, Zambia was sampled to determine whether there are seasonal effects on benthic productivity in Lake Tanganyika. The southern end of the lake is subject to upwelling of nutrient-rich waters during the dry, windy season, and these are known to affect pelagic dynamics (Coulter and Spiegel 1991). This study examined whether these upwelling events might also affect the benthic environment. Possible human impacts at this site include pollution from Mpulungu and the harbour and periodic fishing. However, the sampling site was located at the base of a cliff on the north side of the island, and this location allowed for maximum exposure to the lake and minimized exposure to human influences along the Mpulungu shoreline. The substrate was a rocky talus slope that extended to 16 m depth.

#### *2.1.2 Human impact study*

Mitumba and Mwamgongo were used in a comparative study to examine the effects of human land use change on benthic productivity in Lake Tanganyika. Both sites have similar drainage area, topography, geology, with similar exposure to wind and wave action along the shoreline.

Mitumba (MIT) is the northernmost watershed of Gombe Stream National Park. The watershed is 4.5 km<sup>2</sup> and is almost completely forested. Human impacts are low,

with population densities of  $< 25$  people / km<sup>2</sup>. The substrate was boulders until 3 – 4 m, after which coarse grained sands dominated with large boulders in isolated groups. Mwamgongo (MWA) is the next watershed north of Mitumba. The area of the watershed is approximately 8 km<sup>2</sup> and has been almost completely deforested. Population densities are currently  $> 750$  people/ km<sup>2</sup>. There were numerous boulders until 3 m, isolated rocks and fine grained to muddy sands at 5 – 7 m, and rocks with muddy sediments after 7 – 9 m. All rock surfaces were blanketed with sediment.

## **2.2 Measurements and sampling methodology**

Benthic productivity was measured using oxygen change in light and dark chambers. Chambers were constructed by J.S. MicroProducts, Canada, using clear and opaque plexiglass. The chambers for epilithic productivity covered an area of 0.1 m<sup>2</sup> and held a volume of 0.8 L. The chamber was surrounded by a neoprene skirt that was covered with a lead sock to hold it in place on the rock. The chambers for epipelagic productivity covered an area of 0.09 m<sup>2</sup> and held a volume of 10.8 L. A metal strip on the open edges of the chamber allowed the chamber to be pushed at least 5 cm into the sediment.

Dissolved oxygen was measured using Winkler titration (Stainton et al. 1977). The water in each chamber was stirred with an interior manual paddle before samples were taken through a serum stopper using a needle and 50 ml syringe. Water samples were fixed with an injection of 0.5 ml of MnSO<sub>4</sub> and 0.5 ml of alkaline iodide while in the syringe. Upon return to the laboratory, 0.5 ml of concentrated sulfuric acid was added and the sample was titrated using 0.025 N sodium thiosulphate. Incubations were done at around solar noon for 10 to 25 minutes, depending upon depth, with the shorter times for the shallower depths. In order to allow for acclimation, opaque chambers were placed at least 30 minutes before sampling began. Carbon fixation and respiration were calculated from the oxygen changes assuming a photosynthetic quotient of one.

To avoid the development of an extensive boundary layer and oxygen supersaturation, incubations were done for as short a time as possible, ranging from 4 minutes at 1 m to

40 minutes at 16 m. In deeper water, productivity rates are slower because there is less available light; thus a longer time period was required to measure significant differences in initial and final oxygen concentrations. Water temperatures in Lake Tanganyika are high (c. 25 - 28 °C), and ambient oxygen concentration is near 100% saturation. Even with short incubation times it was difficult to avoid supersaturation and bubble formation in the chambers. The temperature inside the chambers would increase by up to 2 °C during shallow water incubations, making supersaturation inevitable under the high productivity conditions associated with these depths. The loss of dissolved oxygen to bubble formation suggests that the results are likely to underestimate actual epilithic productivity. Light profiles were taken during or immediately following incubation.

Chlorophyll content was used as measure of algal biomass. Algal scrapings were taken from the rock inside each chamber using a brush-syringe scraper constructed by J. S. Microproducts. Scrapings covered an area of 10.1 cm<sup>2</sup> and were taken in triplicate from each chamber. Samples were filtered through Whatman GF/C filters and extracted overnight in 90% methanol before being centrifuged and analyzed for chlorophyll and carotenoids (measured at 665 nm and 480 nm respectively; Talling and Driver, 1963). Turbidity of each sample was measured at 750 nm and subtracted from the absorbance values before the pigment concentrations were calculated. Biomass-specific net productivity (BSNP) was calculated by dividing the net productivity measured in a chamber by the algal biomass in that chamber.

Epilithic productivity was measured at 2, 5, and 10 m. Sampling was done approximately every month from November 1997 to July 1998 in Tanzania and once during the wet season (March 1998) and the dry season (July 1998) in Zambia. Epipelagic productivity was measured at 2, 5, and 10 m at the beginning of the wet season at the Tanzanian sites. Epipelagic biomass was determined by extracting pigments from sediment samples using 90% methanol and analyzing as described above.

The amount of inorganic material on the rock surfaces was also examined as possible indicator of increased sediment input from erosion. Rock surfaces were scraped used the scraper described above, and sampled were filtered onto glass fiber filters. These filters were weighed and combusted at 550°C for 4 hours to burn off all organic material. The filters were then reweighed.

### **2.3 Data analysis**

A non-parametric repeated measured test (Wilcoxin Signed-Ranks; (Sokal and Rolf 1981) was used to examine the paired differences between productivity at Mitumba and Mwangongo. ANOVA (SYSTAT 6.0, 1996) was used to look at other differences between both these sites and to look at seasonal differences in the southern end of the lake.

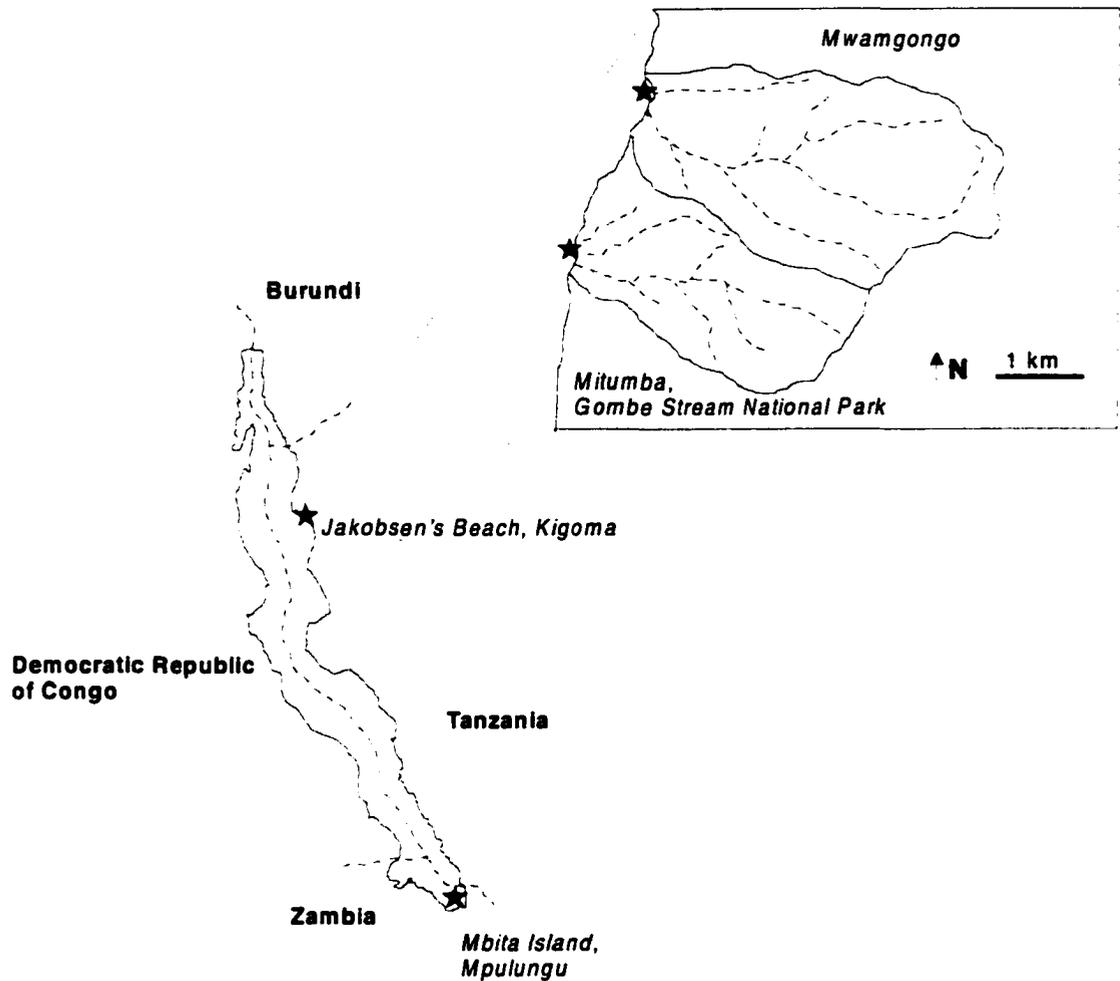


Figure 1. Map of sampling locations. Stars indicate the different sampling locations around the lake. The inset shows a more detailed view of the study areas used for the human impact study. The drainage patterns are included in these watershed basins.

## CHAPTER 3 RESULTS AND DISCUSSION

### 3.1 Seasonal variations—Mbita Island, Mpulungu, Zambia

#### 3.1.1 Productivity

An inter-season comparison of epilithic productivity was made at depths of 1, 2, 3, 5, and 10 m (Table 1). Net productivity ( $p < 0.001$ , ANOVA) and respiration ( $p < 0.01$ , ANOVA) between the two seasons was significantly different.

Table 1. Seasonal average net productivity and respiration during the wet and dry season at Mbita Island, Mpulungu, Zambia (in  $\text{mg O}_2 \text{m}^{-2} \text{hr}^{-1}$ ).

| <i>depth</i> | <i>Net productivity</i> |            | <i>Respiration</i> |            |
|--------------|-------------------------|------------|--------------------|------------|
|              | wet season              | dry season | wet season         | dry season |
| 1            | 189.87                  | 486.43     | 39.54              | 118.86     |
| 2            | 194.05                  | 347.53     | 72.75              | 138.13     |
| 3            | 166.45                  | 196.6      | 31.46              | 69.22      |
| 5            | 88.4                    | 203.25     | 38.71              | 65.97      |
| 10           | 54.11                   | 89.93      | 26.86              | 65.79      |

#### 3.1.2 Biomass

Averaged over all depths, the overall annual average chlorophyll value was 11.31 with a standard deviation of  $7.52 \text{ mg/m}^2$ . Table 2 shows the seasonal average values for each depth. Algal biomass was significantly different with season ( $p < 0.004$ ). Carotenoid ratios had an annual average of 0.50 with a standard deviation of 1.18. The carotenoid ratio was also significantly different with season ( $p < 0.001$ ).

Table 2. Seasonal average values of chlorophyll and the carotenoid ratios at Mbita Island, Mpulungu, Zambia (in mg/m<sup>2</sup>).

| <i>depth</i> | <i>Chlorophyll</i> |            | <i>Chl:carotenoid ratio</i> |            |
|--------------|--------------------|------------|-----------------------------|------------|
|              | wet season         | dry season | wet season                  | dry season |
| 1            | 12.71              | 13.68      | 0.34                        | 0.41       |
| 2            | 12.75              | 10.34      | 0.31                        | 0.41       |
| 3            | 4.03               | 11.10      | 0.10                        | 0.50       |
| 5            | 8.19               | 10.31      | 0.44                        | 0.59       |
| 10           | 11.35              | 10.07      | 0.55                        | 0.77       |

This study suggests that algal productivity is affected by seasonal variations at the south end of the lake. Increases in productivity and biomass during the dry-windy season suggested that the upwelling of nutrient-rich hypolimnetic waters had a considerable influence on periphyton dynamics. Nutrient concentrations increase in the south end of the lake during the dry-windy season, with total phosphorus concentrations tripling and nitrate increasing by 30% (Plisnier et al. 1999). Phytoplankton blooms during this season have been attributed to this increased nutrient availability and can reduce Secchi depths by 10 m (Coulter 1963; Plisnier et al. 1999). This decline in light availability did not appear to reduce productivity over the depths in this study, suggesting that nutrients remained the primary factor limiting algal growth throughout the year.

The pigment concentrations also provided information about seasonal changes in nutrient ratios and light availability affecting the periphyton community. The statistically significant increase in the chlorophyll: carotenoid ratios in the dry-windy season may be caused by increased N-limitation. The surface waters of Lake Tanganyika have low N:P ratios (generally less than 8:1, Hecky et al. 1991), and since upwelling events introduce primarily P, there is a decrease in the average N:P ratio in the south of the lake during the dry-windy season (Plisnier et al. 1999). This may further induce N-limitation, which can

cause an elevation in chlorophyll: carotenoid ratios (Moss 1988; Goericke and Montoya 1998; Holmboe et al. 1999). Changes in the chlorophyll: carotenoid ratios of many algal species may also be caused by light limitation; plants acclimate to shade by increasing the relative amounts of chlorophyll (Galyuon et al. 1996; Gross et al. 1996; Goericke and Montoya 1998). Higher ratios in the dry-windy season may be a response of algal pigments to the reduction in light availability due to phytoplankton blooms.

### *3.1.3 Photoinhibition*

As has generally been reported for periphyton (Hill 1996), there did not appear to be photo-inhibition of net productivity (per unit area) at shallow depths. However, the initial increase in BSNP and BSR with depth suggested that high light intensity may influence algal dynamics at the community level. Algal biomass was relatively higher in the upper few meters, and increasing algal density may have adversely influenced productivity per unit biomass (Hudon et al. 1987). The effect of light may not be apparent per unit area because photo-inhibition may occur only in the upper layers of the algal community with compensation through greater productivity from the more protected underlayer (Boston and Hill 1991). A similar result was noted in Lake Taupo, New Zealand, where Hawes & Smith (1994) proposed that the reduced BSNP in the upper meter was caused by photo-inhibition at the algal community level. In Lake Tanganyika, BSNP increased until 3 m in the wet season but only to 2 m in the dry-windy season. This is consistent with deeper light penetration during the wet season and suggested that photo-inhibition does influence algal community productivity when light intensity was above a certain tolerance level.

## **3.2 Human impact study—Mitumba vs. Mwamgongo**

### *3.2.1 Productivity*

Although there were difference in gross productivity, net productivity did not differ significantly between the two sites (Figure 2 and 3). However, there did appear to be seasonal trends in productivity at 2 m, with much greater productivity at the beginning of

the wet season at MWA, which may be due to an initial flux of allochthonous nutrient input.

Respiration was significantly lower at MWA at 2 m ( $p < 0.0156$ , Wilcoxin Signed-Ranks), but not at 5 m ( $p < 0.0781$ , Wilcoxin Signed-Ranks) or 10 m. The difference in respiration at 2 m is greatest during the wet season, and may actually be due to decay of allochthonous organic matter. Biomass specific net productivity (BSNP) was significantly lower at MWA at 2 m ( $p < 0.0156$ , Wilcoxin Signed-Ranks), 5 m ( $p < 0.0156$ , Wilcoxin Signed-Ranks), and 10 m ( $p < 0.0312$ , Wilcoxin Signed-Ranks). These results suggest that algal productivity is less efficient at the deforested site.

Figure 3 shows net productivity and respiration for 2 m, and Figure 4 shows BSNP for all depths. Average annual net productivity and respiration are shown in Table 3.

Table 3. Average annual epilithic net productivity and respiration for Mitumba, Mwamgongo and Jakobsen's beach (in  $\text{mg O}_2 \text{ m}^{-2} \text{ hr}^{-1}$ ).

| <i>depth</i> | <i>Net productivity</i> |        |        | <i>Respiration</i> |       |       |
|--------------|-------------------------|--------|--------|--------------------|-------|-------|
|              | MIT                     | MWA    | JAK    | MIT                | MWA   | JAK   |
| 2            | 111.18                  | 137.04 | 118.01 | 62.62              | 88.83 | 34.48 |
| 5            | 71.22                   | 70.64  | 100.24 | 44.72              | 34.16 | 24.71 |
| 10           | 56.14                   | 64.53  | 81.21  | 29.21              | 50.28 | 20.90 |

As expected, epipelagic productivity was much lower than epilithic productivity. Average values during the months sampled can be seen in Table 4. Unlike epilithic productivity, the differences between the two sites are not significant.

Table 4. Average annual epipellic net productivity and respiration for Mitumba, Mwamgongo, and Jakobsen's beach (in mg O<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup>).

| <i>depth</i> | <i>Net productivity</i> |       |       | <i>Respiration</i> |       |       |
|--------------|-------------------------|-------|-------|--------------------|-------|-------|
|              | MIT                     | MWA   | JAK   | MIT                | MWA   | JAK   |
| 2            | 60.12                   | 43.42 | 31.23 | 9.48               | 19.86 | 15.30 |
| 5            | 42.10                   | 55.21 | 36.57 | 3.75               | 12.71 | 11.66 |
| 10           | 27.84                   | 33.04 | 54.33 | 4.25               | 4.91  | 12.78 |

### 3.2.2 Biomass

Chlorophyll *a* and the carotenoid ratio are significantly greater at the deforested site at all depths ( $p < 0.0$ , ANOVA). Over all depths, averaged annual chlorophyll was  $7.04 \pm 3.52$  mg/m<sup>2</sup> for Mitumba and  $28.89 \pm 8.08$  mg/m<sup>2</sup> for Mwamgongo. Carotenoid ratios were  $0.63 \pm 0.17$  and  $1.02 \pm 0.10$  respectively (Table 5).

Table 5. Average annual chlorophyll (in mg/m<sup>2</sup>) and carotenoid ratios for Mitumba and Mwamgongo.

| <i>depth</i> | <i>Chlorophyll</i> |       | <i>Chl:carotenoid ratio</i> |      |
|--------------|--------------------|-------|-----------------------------|------|
|              | MIT                | MWA   | MIT                         | MWA  |
| 2            | 5.59               | 29.64 | 0.43                        | 0.95 |
| 5            | 5.19               | 31.18 | 0.68                        | 1.08 |
| 10           | 10.42              | 25.85 | 0.78                        | 0.88 |

### 3.2.3 Ambient oxygen

Dissolved oxygen (DO) concentrations varied at each of the study sites (Table 6). The water was usually near 100% saturation. Ambient DO in the water column was significantly lower at Mwamgongo than at Mitumba ( $p < 0.025$ , ANOVA). As water temperature and wave action are similar at each site, this decline in DO must reflect increased biological and/or chemical oxygen demand in the water column. Erosion increases the flux of allochthonous organic matter into a lake, and the decay of this

material may be the cause of the lower oxygen levels. The higher values at Mpulungu reflect the fact that this location experiences a greater temperature range, since the upwelling water is typically around 2 °C lower than the surface waters of lake.

Table 6. Average annual dissolved oxygen concentrations for the study sites (in mg/L).

| <i>depth</i> | MIT  | MWA  | JAK  | MPU  |
|--------------|------|------|------|------|
| 2            | 6.82 | 6.02 | 5.98 | 7.52 |
| 5            | 6.58 | 5.71 | 5.91 | 7.03 |
| 10           | 6.39 | 5.71 | 5.75 | 7.08 |

#### 3.2.4. Light

There are no significant differences between light attenuation at Mitumba and Mwamgongo. A logarithmic regression fit to the annual average light profiles shows that in general, the forested site has better light penetration (Figure 5).

Unfortunately, light profiles were taken from the boat, which usually anchored further offshore at the disturbed site than at the forested one. Visibility while diving was lower at Mwamgongo than at Mitumba, declining to 1.5 m at 2 m depth in wavy conditions. Mwamgongo has smaller grain sizes which are more prone to resuspension through wave action. Also, since light profiles were rarely taken at both sites on the same day, it is difficult to make actual comparisons.

The relationship of light with net productivity shows further differences between the two sites (Figure 6). The regression lines for each site are significantly different, and the difference in slopes suggests that algal growth may be affected by light availability ( $p < 0.001$ ). In particular, a small increase in light produces a much greater increase in net productivity at Mwamgongo, implying that light limitation now prevails to a greater extent than at Mitumba. The higher productivity levels seen at Mwamgongo are likely

due to increased nutrient availability. In general, light levels required for algal growth are relatively low, compared with surface light (Hill 1996). Due to its equatorial location, light should not be a limiting factor in primary productivity in Lake Tanganyika, except for algae at great depths. The depth of the littoral zone generally extends to around 30 m (Coulter 1991). Therefore, the low light levels and greater influence of light availability at Mwamgongo suggest greater suspended particulate matter at this site.

### *3.2.5. Settled sediment*

Rock surfaces at the deforested site showed significantly higher amounts of inorganic material than rock surfaces at the forested site ( $z$ -test;  $z = 3.89$ ;  $p < .0001$ ) (Figure 7). This suggests that deforestation is associated with increased erosion and the input of significant amounts of sediment along the lake shoreline. This sediment can have a negative effect on the biota, as it fills in potential habitat in rocky areas and can interfere with feeding for grazing species. These results are consistent with those of the light profiles, which suggested increased suspended sediment.

## **3.3 Comparison with benthic productivity in other lakes**

The data in this study compares well with previous studies of epilithic productivity on Lake Tanganyika. Takamura (1988) found average values of 43 – 52.4 mg C m<sup>-2</sup> hr<sup>-1</sup> for epilithic algae at depths of 1.5 and 4.5 m at Mbemba, Democratic Republic of Congo in the dry-windy season, whereas this study found productivity rates of 77.06 – 79.01 mg C m<sup>-2</sup> hr<sup>-1</sup> for similar depths in the south of the lake and slightly lower values in the Kigoma area. This discrepancy is consistent with the hydrodynamics of the lake basin. Seasonal upwellings are not as extensive in the north (Coulter and Spigel 1991), and thus it might be expected that average net productivity values from that area of the lake are lower. This suggests that upwelling events and vertical mixing provide an important source of nutrients for primary productivity in Lake Tanganyika.

As expected, benthic productivity in Lake Tanganyika is high when compared to temperate lakes (Figure 8). Daily epilithic productivity rates in Lake Tanganyika does

not differ greatly from that of other large oligotrophic lakes. Daily photosynthetic areal growth rates are similar to those in Lake Thingvallavatn, Iceland and Georgian Bay, Lake Huron and higher than that of ultra-oligotrophic Lake Tahoe and Crater Lake (Loeb et al. 1982; Duthie and Jones 1990; St. Jonsson 1992). The relatively high value for Lake Malawi is based on only one datum (Bootsma 1993), and subsequent work may find that epilithic productivity is similar to that of Lake Tanganyika. However, since algal biomass is low, Lake Tanganyika does have a BSNP which is 2 – 6 times that of the other lakes, with the only exceptions being depths 5 m and 10 m in the Georgian Bay which have a similar BSNP. Although Lake Taupo, New Zealand has extremely high areal algal growth rates, it also has unusually high algal biomass (160 – 500 mg chl m<sup>-2</sup>) and thus low BSNP (Hawes and Smith 1994).

There do not appear to be any latitudinal patterns to epilithic productivity among these lakes. This is surprising, since the higher temperatures and greater available light found in the tropics generally stimulate primary productivity (Lewis 1987), and these lakes do show a general trend of increasing phytoplankton productivity with decreasing latitude. Although it does vary among these lakes, nutrient concentration does not correlate with epilithic productivity. This suggests that neither ambient irradiance nor open-water nutrient concentrations are the primary factors influencing benthic algal dynamics. However, the temperature variation associated with latitudinal change may be important. Higher temperatures increase microbial activity, which would lead to more rapid nutrient cycling within the algal mat (Lewis 1987). This may be an considerable source of nutrients for periphyton and a reason for the higher BSNP found in Lake Tanganyika. Wave action and grazer impact may also be important factors influencing the periphyton community, particularly in Lake Tanganyika, where the wave base is relatively deep and the primary consumer level consists of a high diversity and density of species.

## **CHAPTER 4 CONCLUSIONS**

### **4.1 Seasonal variation in benthic productivity**

Seasonal upwellings do appear to influence benthic productivity in the southern end of Lake Tanganyika. There are significant changes in net productivity, respiration, and algal biomass during the dry season. Although light penetration must decrease due to phytoplankton blooms, this does not appear to be affecting benthic productivity at the depths studied.

The values for periphyton net productivity compare well with those found for the northwest coast. Takamura (1988) recorded average values that are about 30% lower than those found in this study. This is consistent with the hydrodynamics of the lake basin. Seasonal upwellings are not as extensive in the north, and thus it might be expected that the average net productivity values are lower.

### **4.2 Effects of deforestation**

Deforestation clearly affects benthic productivity. The results of this study suggest that erosion has increased the input of sediments, nutrients, and organic matter into the lake. Changes in light attenuation and the influence of light availability on algal productivity may be due to increased suspended sediments. Increased benthic respiration and lower ambient dissolved oxygen concentration are likely due to decay of organic matter, which may be of allochthonous origin. However, the increased benthic respiration seen at the deforested site may be because of increased algal stress and less efficient productivity.

In addition, increased sediment inputs from deforestation may reduce the amount of habitat available for colonization. If settling rates are high enough, existing algae will be covered by sediment particles, effectively removing these areas from recolonization. Large volumes of sediment may decrease the nutritive value of this food source and reduce the feeding efficiency of benthic grazers and deposit feeders.

### **4.3 Directions for future work**

There are a number of studies that would increase our understanding of how increased sediment input may be affecting Lake Tanganyika. Probably the most important of these is whether deforestation is accompanied by changes in nutrient concentrations and sediment-nutrient interactions both in the water column and in the sediment substrate. Although we can assume that deforestation would also affect epipelagic productivity, the magnitude of this affect remains unclear. Current data is too sparse to show any statistical trends.

Finally, these changes in the benthic habitat represent changes in food quality and quantity. Other studies have documented changes in upper trophic levels that are correlated with changes in land use patterns (Alin et al. 1999), but whether this is caused by changes in food web structure or by changes in habitat is unknown. This has important implications for conservation measures in the lake.

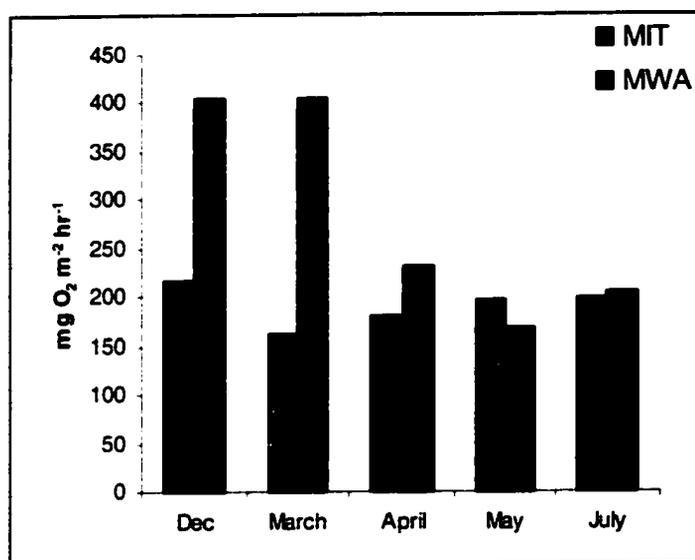
**FIGURES**

Figure 2. Seasonal variation in gross productivity at 2 m at Mitumba and Mwangongo.

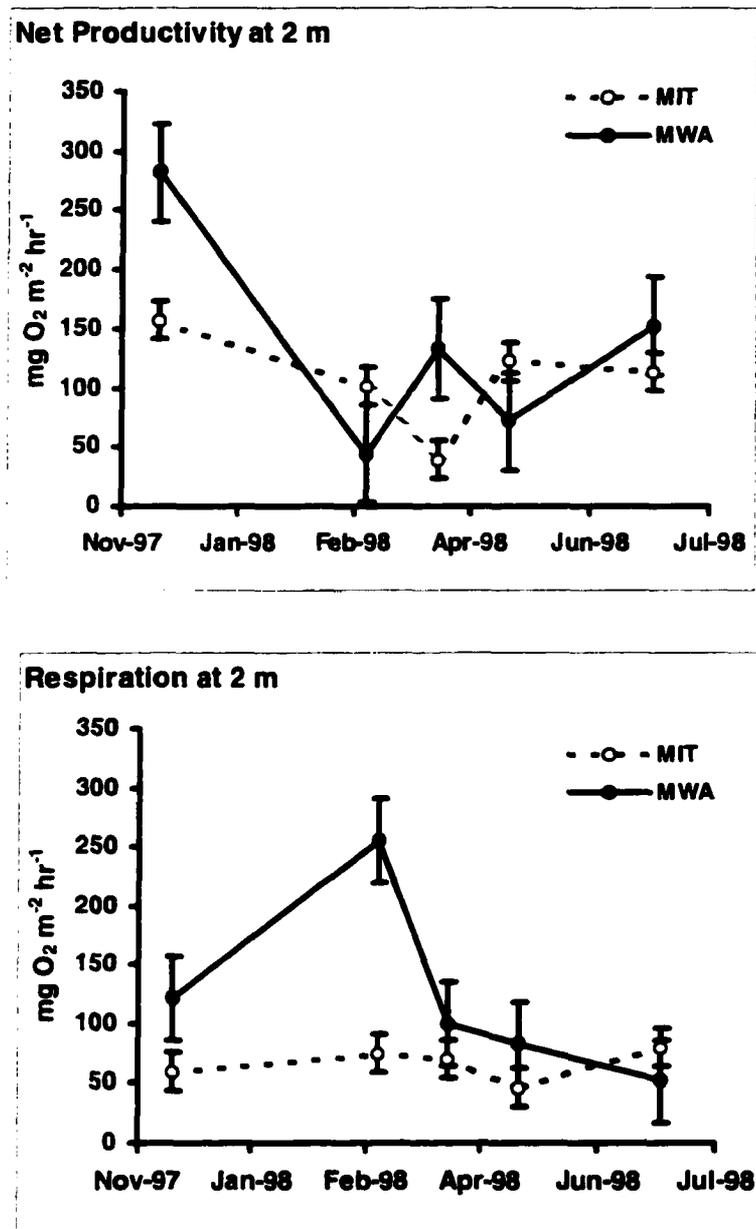


Figure 3. Net productivity and respiration at 2 m throughout the sampling period at Mitumba and Mwamgongo. Error bars represent one standard error.

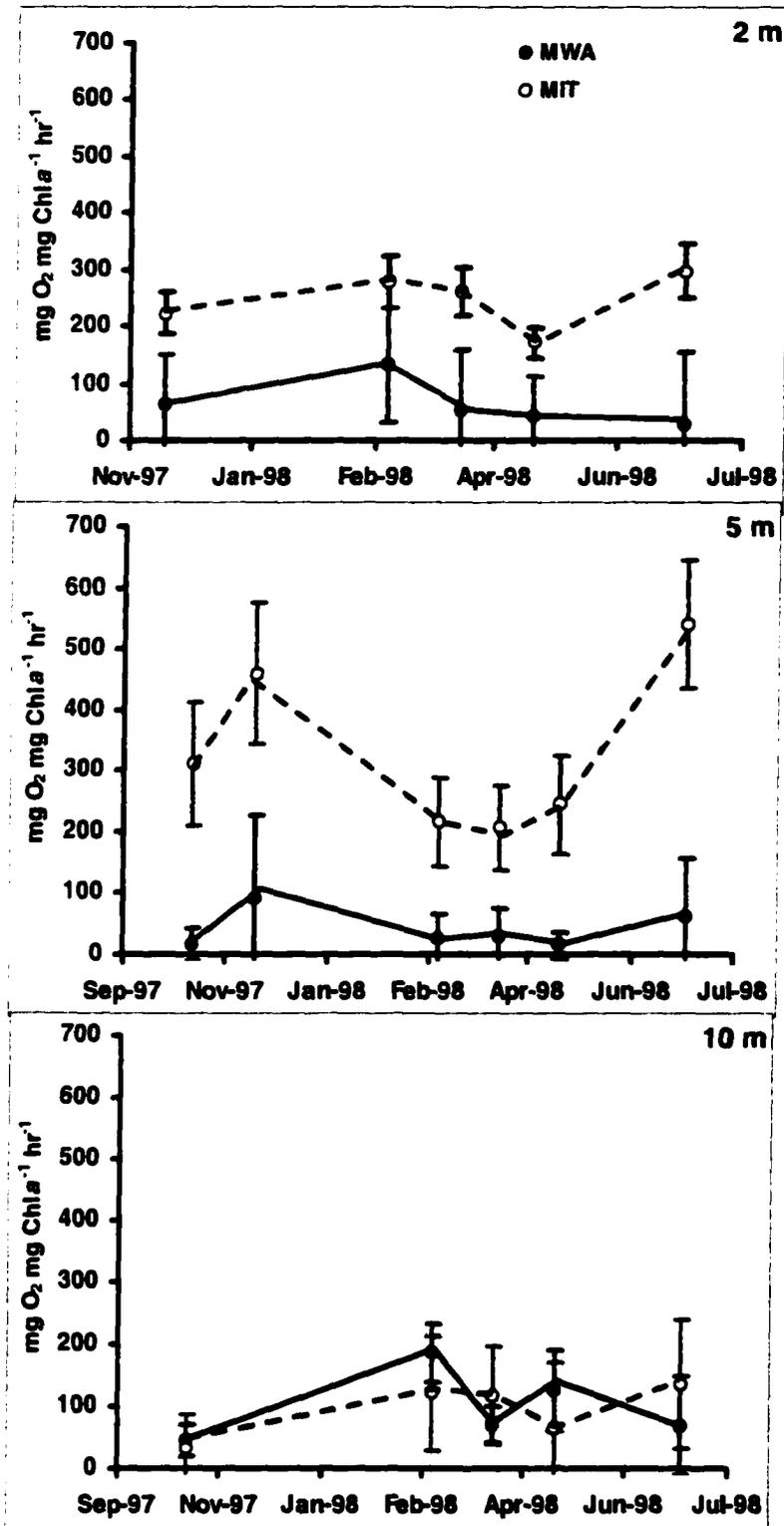


Figure 4. BSNP at Mitumba and Mwamgongo. Error bars represent one standard error.

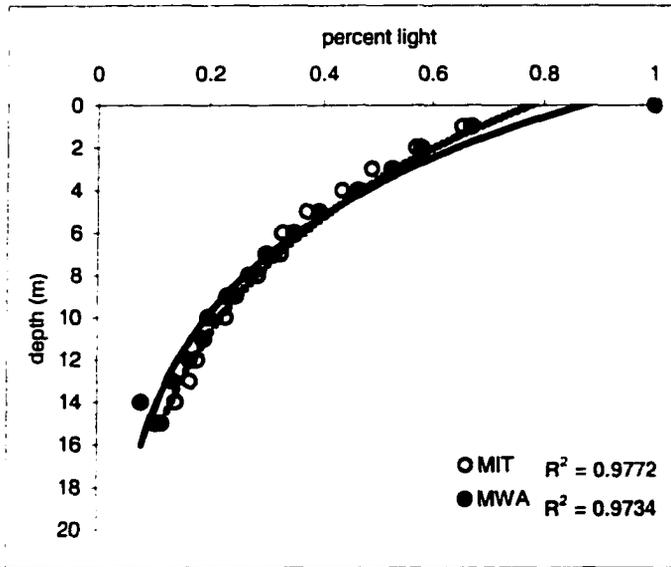


Figure 5. Average annual light at Mitumba and Mwamongo. This profile shape did not change significantly throughout the year.

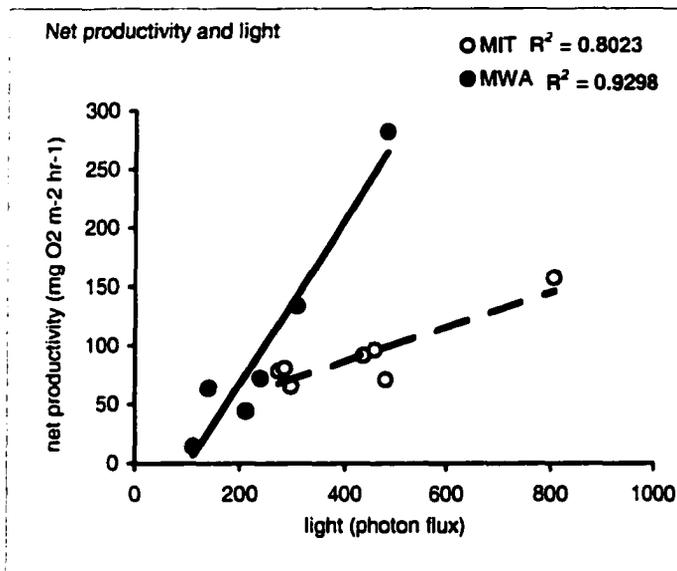


Figure 6. Net productivity and light for Mitumba and Mwamongo. The regression lines for each site are significantly different.

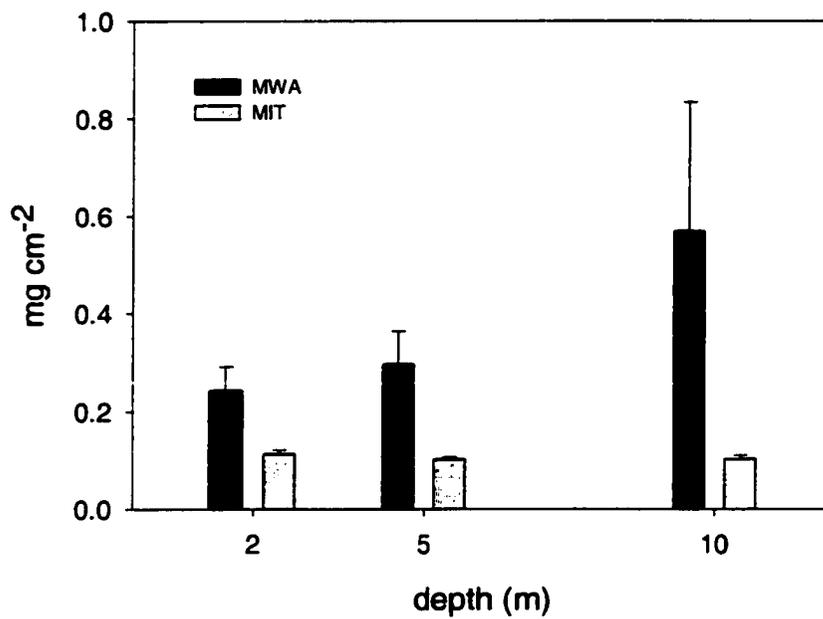


Figure 7. Sediment on rock surfaces at Mitumba and Mwamongo. Error bars represent one standard error.

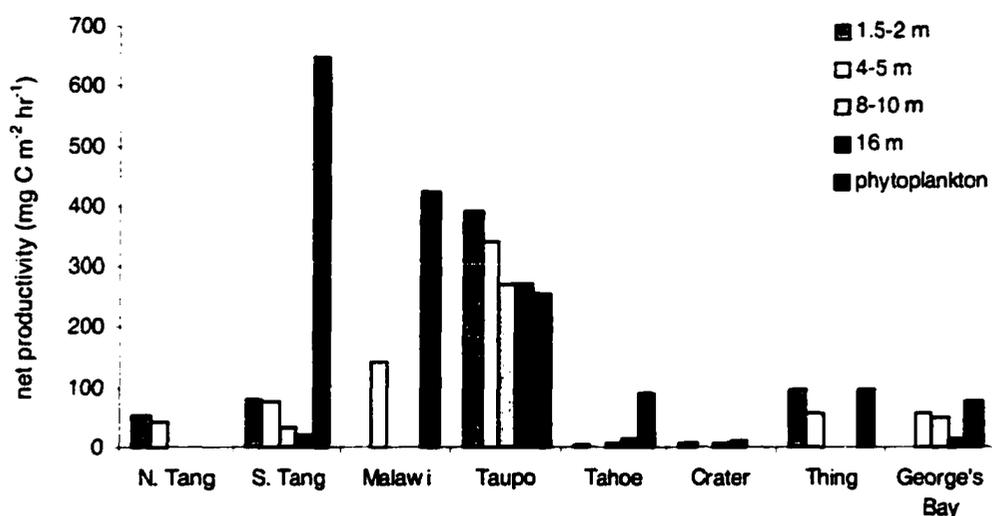


Figure 8. A comparison of epilithic net productivity among large, oligotrophic lakes. Data for southern Lake Tanganyika (S. Tang.) are from this study. Sources (with abbreviations used in the figure) for the other data are as follows: North Tanganyika (N. Tang.) (Takamura 1988); Lake Malawi (Bootsma 1993); Lake Tahoe and Crater Lake, North America, (Loeb et al. 1982); Lake Taupo, New Zealand (Hawes and Smith 1994); Lake Thingvallavatn (Thing.), Iceland, (St. Jonsson 1992); George's Bay, Lake Huron, North America, (Duthie and Jones 1990). For phytoplankton data: Lake Tanganyika (Sarvala et al. 1999); Lake Malawi (Patterson and Kachinjika 1995); Lake Tahoe (Goldman 1988); Crater Lake (Loeb et al. 1982); Lake Taupo (Hawes and Smith 1994); Lake Thingvallavatn (Jonasson et al. 1992); George's Bay, (Duthie and Jones 1990).

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## **APPENDIX C: SEASONAL DYNAMICS OF PERIPHYTON IN A LARGE TROPICAL LAKE, LAKE TANGANYIKA, EAST AFRICA**

### **Abstract**

This study examines seasonal variation in epilithic algal dynamics in southern Lake Tanganyika, East Africa. Temporal variation in epilithic productivity in Lake Tanganyika is substantially influenced by the seasonal patterns in lake hydrodynamics. Increased upwelling of nutrient-rich water during the dry-windy season corresponded with significantly greater epilithic biomass and productivity. An increase in the chlorophyll: carotenoid ratio during the dry-windy season indicated both reduced light availability and increased N-limitation. Although it supports much of the lake's biological diversity, epilithic algae make a minor contribution to the total energy budget in Lake Tanganyika. A comparison among large, oligotrophic lakes revealed no significant latitudinal trends in periphyton productivity or biomass. However, Lake Tanganyika has relatively low epilithic algal biomass and therefore a much higher biomass specific net productivity than temperate lakes. The influence of wave action and consumer density and diversity may be important in moderating productivity of the epilithic community.

### **Introduction**

Studies of primary productivity in aquatic systems often concentrate on phytoplankton communities and ignore possible contributions from periphyton. Although the area of the littoral zone is usually small compared to the volume of the

pelagic, benthic productivity rates are frequently higher than rates among the plankton. Periphyton have an advantage over phytoplankton since they have access to additional nutrients in sedimentary material (Stevenson et al. 1996). In oligotrophic lakes, where nutrient concentrations in the water column are low and the photic zone is relatively deep, periphyton productivity may be an important contributor to fixed carbon (Loeb et al. 1982; Hawes and Smith 1994; Hecky and Hesslein 1995). This additional primary resource provides a niche for exploitation, increasing biodiversity and promoting speciation through competition and specialization (Bootsma et al. 1996; Genner et al. 1999). The littoral zone often serves as the breeding grounds for pelagic species and provides habitat during the larval or juvenile stage of their life cycle. Energy transfers within this zone can have an important impact on whole-lake processes (MacIntyre and Melack 1995; Schindler et al. 1996).

Lake Tanganyika, East Africa, provides an ideal environment in which to examine seasonality of periphyton productivity in a tropical system. Lake Tanganyika is a large (mean width 50 km; length 650 km; mean and maximum depths 570 m and 1470 m), oligotrophic, and permanently stratified lake located a few degrees south of the equator (Coulter and Spigel 1991). The clarity of the water allows for light penetration up to 30 m (Hecky et al. 1991), creating a relatively deep littoral area and a large amount of habitat available for colonization by periphyton. A preliminary study at the lake's northern end suggested that periphyton contribute substantially to littoral zone productivity and play an important role in the littoral food web (Takamura 1988). The littoral zone of Lake Tanganyika contains one of the world's most diverse freshwater

faunas, and this diversity has been attributed in part to food partitioning of this periphyton resource (Bootsma et al. 1996).

A monsoonal climate creates a large seasonal hydrodynamic pattern in the lake. During the dry-windy season from May to August, strong southerly winds tilt the permanent thermocline and cause upwelling of the deeper nutrient-rich waters at the south end of the lake. Increased nutrient availability from these upwelling events produces phytoplankton blooms that can dramatically reduce water clarity (Plisnier et al. 1999). These changes impact upper trophic levels at the southern end of the lake and are reflected as seasonal patterns in community dynamics among pelagic fish species (Phiri and Shirakihara 1999). If they exist, seasonal fluctuations in this primary resource may influence the littoral food web, generating a larger scale seasonal pattern in this tropical system (Thompson and Townsend 1999).

This study examined seasonal variation in benthic algal dynamics at the southern end of Lake Tanganyika. Since much of the lake shoreline is rocky, and it is these rocky areas that support the greatest biological diversity, this study focuses on epilithic algae and their relative contribution to total primary productivity in Lake Tanganyika. I hypothesized that periphyton productivity in the south would show fluctuations related to the seasonal patterns in lake hydrodynamics, with greater productivity evident during the dry-windy season. The greater nutrient availability from these upwellings would lead to higher average annual productivity rates than those measured for benthic algal communities in the north of the lake. Furthermore, I postulated that these seasonal changes in nutrient availability would be reflected as changes in the chlorophyll:

carotenoid ratios of the algal community. Since light intensity is high in the tropics, I expected to find evidence for photo-inhibition of epilithic productivity at shallow depths.

## **Methods**

### *Study site*

Although upwelling may increase productivity in the dry-windy season, increased allochthonous nutrient inputs during the rainy season may also increase productivity, possibly dominating any autochthonous seasonal signal. To minimize terrestrial influences, the chosen study site was located at the base of a cliff on the northern side of Mbita Island, Mpulungu, Zambia (Figure 1). This location ensured that the site had maximum exposure to the lake and that changes in nutrient concentration would be due to upwelling events rather than increased terrestrial inputs during the wet season. Since traditional local beliefs prohibit habitation of the island, human impacts are low and fishing at this location is minimal. Substrate ranged in size from small pebbles to boulders with a steep slope to 16 m after which it became a level coarse grained sand surface.

### *Measurements*

Epilithic net productivity and respiration were measured *in situ* using oxygen change in clear and opaque chambers. Carbon fixation and respiration were calculated from the oxygen changes assuming a photosynthetic quotient of one. The chambers were constructed by J. S. Microproducts (East St. Paul, Manitoba, Canada) and covered a

surface area of  $0.01 \text{ m}^2$  with a volume of 0.8 L. Chambers were held to the rock surface by a lead sock placed over a neoprene skirt adhered to the bottom of the chambers. In order to allow for acclimation, opaque chambers were placed at least 30 minutes before sampling began. The water in each chamber was stirred with an interior manual paddle before samples were taken through a serum stopper using a needle and 50 ml syringe. Measurements were made along a transect at depths of 1, 2, 3, 5, and 10 m during both the wet (March) and dry-windy (July) season, and additionally at 16 m during the dry-windy season. Over a period of two weeks during each season, measurements were made almost daily at each depth with one to four replications each day.

To avoid the development of an extensive boundary layer and oxygen supersaturation, incubations were done for as short a time as possible, ranging from 4 minutes at 1 m to 40 minutes at 16 m. In deeper water, productivity rates are slower because there is less available light; thus a longer time period was required to measure significant differences in initial and final oxygen concentrations. Water temperatures in Lake Tanganyika are high (c. 25 - 28 °C), and ambient oxygen concentration is near 100% saturation. Even with short incubation times it was difficult to avoid supersaturation and bubble formation in the chambers. The temperature inside the chambers would increase by up to 2 °C during shallow water incubations, making supersaturation inevitable under the high productivity conditions associated with these depths. The loss of dissolved oxygen to bubble formation suggests that the results are likely to underestimate actual epilithic productivity, providing a conservative test for the hypothesis of increased productivity during the dry-windy season.

Dissolved oxygen concentrations were determined using Winkler titration (Stainton et al. 1977). Dissolved oxygen was immediately precipitated as a manganese oxide in the syringes using  $MnSO_4$  and alkaline iodide. This stabilized the oxygen concentrations, reducing the time pressure to analyze the samples before significant changes in oxygen concentrations occurred. The samples were stored with ice until return to the laboratory where the titrations were completed. This method allowed for more accurate measurements and greater precision than completing the titrations in the field.

Chlorophyll content was used as measure of algal biomass. Algal scrapings were taken from the rock inside each chamber using a brush-syringe scraper constructed by J. S. Microproducts. Scrapings covered an area of  $10.1 \text{ cm}^2$  and were taken in triplicate from each chamber. Samples were filtered through Whatman GF/C filters and extracted overnight in 90% methanol before being centrifuged and analyzed for chlorophyll and carotenoids (measured at 665 nm and 480 nm respectively; Talling & Driver, 1961). Turbidity of each sample was measured at 750 nm and subtracted from the absorbance values before the pigment concentrations were calculated. Biomass-specific net productivity (BSNP) was calculated by dividing the net productivity measured in a chamber by the algal biomass in that chamber.

Data were log transformed for statistical analyses using multiple regression models. All statistics were done using JMP IN.

## Results

### *Productivity and respiration*

There were significant seasonal differences in net productivity and respiration of epilithic algae at Mbita Island (Figure 2). In the dry-windy season, net productivity was significantly higher ( $p < 0.0001$ ;  $F_{2, 131} = 56$ ), and respiration was significantly higher ( $p < 0.0001$ ;  $F_{2, 113} = 13$ ). Net productivity was significantly correlated with both depth ( $p < 0.0001$ ;  $t = -8.54$ ) and season ( $p < 0.0001$ ;  $t = 5.08$ ). Respiration was also significantly related to depth ( $p < 0.0001$ ;  $t = -4.34$ ) and season ( $p < 0.0016$ ;  $t = 3.23$ ). Net productivity and respiration at 16 m during the dry-windy season averaged  $49 \pm 10$  and  $36 \pm 26$  mg O<sub>2</sub> m<sup>-2</sup> hr<sup>-1</sup> respectively.

### *Biomass*

Algal pigments showed differences in community biomass between the two seasons (Figure 2). Algal biomass (chlorophyll) was significantly higher during the dry-windy season ( $p < 0.0001$ ;  $F_{2, 269} = 10$ ). The chlorophyll: carotenoid ratios were also significantly higher during the dry-windy season ( $p < 0.0001$ ;  $F_{3, 269} = 36$ ). For chlorophyll: carotenoid ratios depth ( $p < 0.0001$ ;  $t = 7.90$ ), season ( $p < 0.0001$ ;  $t = 4.79$ ) and the interaction between depth and season ( $p < 0.0368$ ;  $t = -2.10$ ) were significant in the multiple regression model. Chlorophyll concentrations at 16 m were  $25 \pm 3$  mg m<sup>-2</sup> and the chlorophyll: carotenoid ratio was  $0.9 \pm 0.05$ . Biomass specific net productivity increased with depth until 3 m in the wet season and 2 m in the dry-windy season, after which it declined with depth in both seasons (Figure 2). The difference in BSNP between

seasons and across depths was not significant.

## **Discussion**

Seasonal variations in primary productivity are more visible in temperate lakes, where annual patterns in light and temperature have a major influence on lake dynamics. The lack of a strong annual cycle to these variables in the tropics has led to the common misperception of a lack of seasonality in tropical ecosystems (Lewis 1987). However, the results suggest that there are strong seasonal patterns in epilithic algal dynamics at the southern end of Lake Tanganyika.

Epilithic algae were strongly affected by seasonal variations in hydrodynamics at the south end of Lake Tanganyika. Increases in productivity and biomass during the dry-windy season suggested that the upwelling of nutrient-rich hypolimnetic waters had a considerable influence on periphyton dynamics. Nutrient concentrations increase in the south end of the lake during the dry-windy season, with total phosphorus concentrations tripling and nitrate increasing by 30% (Plisnier et al. 1999). Phytoplankton blooms during this season have been attributed to this increased nutrient availability and can reduce Secchi depths by 10 m (Coulter 1963; Plisnier et al. 1999). This decline in light availability did not appear to reduce productivity over the depths in this study, suggesting that nutrients remained the primary factor limiting algal growth throughout the year.

As has generally been reported for periphyton (Hill 1996), there did not appear to be photo-inhibition of net productivity (per unit area) at shallow depths. However, the initial increase in BSNP and BSR with depth suggested that high light intensity may

influence algal dynamics at the community level. Algal biomass was relatively higher in the upper few meters, and increasing algal density may have adversely influenced productivity per unit biomass (Hudon et al. 1987). The effect of light may not be apparent per unit area because photo-inhibition may occur only in the upper layers of the algal community with compensation through greater productivity from the more protected underlayer (Boston and Hill 1991). A similar result was noted in Lake Taupo, New Zealand, where Hawes & Smith (1994) proposed that the reduced BSNP in the upper meter was caused by photo-inhibition at the algal community level. In Lake Tanganyika, BSNP increased until 3 m in the wet season but only to 2 m in the dry-windy season. This is consistent with deeper light penetration during the wet season and suggested that photo-inhibition does influence algal community productivity when light intensity was above a certain tolerance level.

The pigment concentrations also provided information about seasonal changes in nutrient ratios and light availability affecting the periphyton community. The statistically significant increase in the chlorophyll: carotenoid ratios in the dry-windy season may be caused by increased N-limitation. The surface waters of Lake Tanganyika have low inorganic N:P ratios (generally less than 8:1; Hecky, 1991), and since upwelling events introduce primarily P, there is a decrease in the average N:P ratio in the south of the lake during the dry-windy season (Plisnier et al. 1999). This may further induce N-limitation, which can cause an elevation in chlorophyll: carotenoid ratios (Moss 1988; Goericke and Montoya 1998; Holmboe et al. 1999). Changes in the chlorophyll: carotenoid ratios of many algal species may also be caused by light limitation; plants acclimate to shade by

increasing the relative amounts of chlorophyll (Galyuon et al. 1996; Gross et al. 1996; Goericke and Montoya 1998), and the higher ratios in the dry-windy season may be a response of algal pigments to the reduction in light availability due to phytoplankton blooms. The increase the ratios may also be due to some combination of N-limitation and reduced light.

#### *Primary productivity in Lake Tanganyika*

The values for epilithic net productivity in the south of the lake are about 50% higher than those found in the study done on the northwest shoreline. Takamura (1988) found average values of 43 – 52.4 mg C m<sup>-2</sup> hr<sup>-1</sup> for epilithic algae at depths of 1.5 and 4.5 m in the dry-windy season, whereas this study found productivity rates of 77.06 – 79.01 mg C m<sup>-2</sup> hr<sup>-1</sup> for similar depths. This discrepancy is consistent with the hydrodynamics of the lake basin. Seasonal upwellings are not as extensive in the north (Coulter and Spigel 1991), and thus it might be expected that average net productivity values are lower. This suggests that upwelling events and vertical mixing provide an important source of nutrients for primary productivity in Lake Tanganyika.

#### *Comparison with other lakes*

Daily epilithic productivity rates in Lake Tanganyika does not differ greatly from that of other large oligotrophic lakes (Figure 3). Daily photosynthetic areal growth rates are similar to those in Lake Thingvallavatn, Iceland and Georgian Bay, Lake Huron and higher than that of ultra-oligotrophic Lake Tahoe and Crater Lake (Loeb et al. 1982;

Duthie and Jones 1990; St. Jonsson 1992). The relatively high value for Lake Malawi is based on only one datum (Bootsma 1993), and subsequent work may find that epilithic productivity is similar to that of Lake Tanganyika. However, since algal biomass is low, Lake Tanganyika does have a BSNP which is 2 – 6 times that of the other lakes, with the only exceptions being depths 5 m and 10 m in the Georgian Bay which have a similar BSNP. Although Lake Taupo, New Zealand has extremely high areal algal growth rates, it also has unusually high algal biomass (160 – 500 mg chl m<sup>-2</sup>) and thus low BSNP (Hawes and Smith 1994).

There do not appear to be any latitudinal patterns to epilithic productivity among these lakes. This is surprising, since the higher temperatures and greater available light found in the tropics generally stimulate primary productivity (Lewis 1987), and these lakes do show a general trend of increasing phytoplankton productivity with decreasing latitude (Figure 3). Although it does vary among these lakes, nutrient concentration does not correlate with epilithic productivity. This suggests that neither ambient irradiance nor open-water nutrient concentrations are the primary factors influencing benthic algal dynamics. However, the temperature variation associated with latitudinal change may be important. Higher temperatures increase microbial activity, which would lead to more rapid nutrient cycling within the algal mat (Lewis 1987). This may be an considerable source of nutrients for epilithon and a reason for the higher BSNP found in Lake Tanganyika.

Instead, epilithic productivity may be more influenced by factors that have a direct impact on attached algae, such as wave action. Wave action has been invoked as a loss

mechanism to explain lower algal biomass in some lakes, particularly at shallow depths (Duthie and Jones 1990). Waves also play the additional role of reducing the boundary layer and increasing access to nutrients. With a wave base of at least 5 m, water movement could have substantial control over periphyton nutrient access in Lake Tanganyika. Although storm activity during the wet season would periodically deepen the wave base, the persistent winds during the dry-windy season likely lead to a constant, deeper wave base. The resulting reduction in the boundary layer may be important in maintaining high CO<sub>2</sub> concentrations and removing oxygen during this nutrient-rich period. Wave activity has also been invoked as an influential factor in the Georgian Bay, which also has high BSNP (Duthie and Jones 1990).

Consumer density and diversity have also been implicated in the regulation of primary productivity. Grazing decreases the boundary layer, eliminates detritus and dead algal cells, and increases nutrient availability. In addition to other primary consumers, the study site had at least 6 snail species at relatively high densities (28.4 snails/m<sup>2</sup>, SE = 1.4, n = 109) and up to 10 species of cichlid grazers (Hori et al. 1995). This consumer species richness may be one of the reasons for the low algal biomass in Lake Tanganyika (Naeem and Li 1998). Grazers have been found to influence productivity in Lake Tahoe and have been implicated in maintaining nutrient availability for epilithic algae in Lakes Tahoe (Flint and Goldman 1975), Thingvallavatn (St. Jonsson 1992) and Malawi (Andre 1999). A combination of wave action and consumer impact can be invoked to explain the high net productivity for Lake Taupo, which has low wave action, low grazer density, and exceptionally high algal biomass (Hawes and Smith 1994).

## **Conclusion**

This study documented significant temporal variability in epilithic algal dynamics in Lake Tanganyika at the seasonal scale. Increased upwelling during the dry-windy season led to increases in periphyton biomass and productivity. Changes in the chlorophyll: carotenoid ratios of the algal community indicate the concomitant seasonal variation in light and nutrient availability.

Although epilithic algal productivity (per unit area) is similar to that in other large oligotrophic lakes, relatively low biomass produces high biomass specific net productivity. Latitudinal trends in epilithic productivity and biomass were not apparent among large oligotrophic lakes, suggesting that factors other than temperature and irradiance may control periphyton community dynamics. Wave action and grazer impact may be important factors influencing the periphyton community, particularly in Lake Tanganyika, where the wave base is relatively deep and the primary consumer level consists of a high diversity and density of species.

The high productivity rates in the littoral zone support a diverse range of taxa. Seasonal patterns in the pelagic species dynamics at the south end of the lake have been documented, and breeding and the juvenile stage of some of these species occurs in the littoral zone (Coulter 1991). Although it is currently unknown, rock-dwelling cichlid species probably breed continuously with peaks of activity (P. Reinthal, pers. com). For the south end of Lake Tanganyika, these breeding pulses may occur in conjunction with seasonal patterns of periphyton productivity, particularly among the herbivorous species.

Understanding the underlying dynamics of primary productivity in the littoral zone may provide information about community structure and function of the upper trophic levels in Lake Tanganyika.

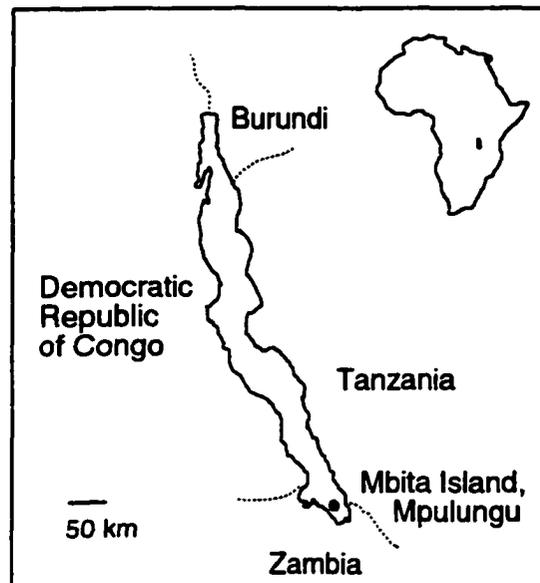


Figure C.1. Location of the study site. Lake Tanganyika is located between 4 and 9°S in East Africa. The study was conducted on the north side of Mbita Island near Mpulungu, Zambia.

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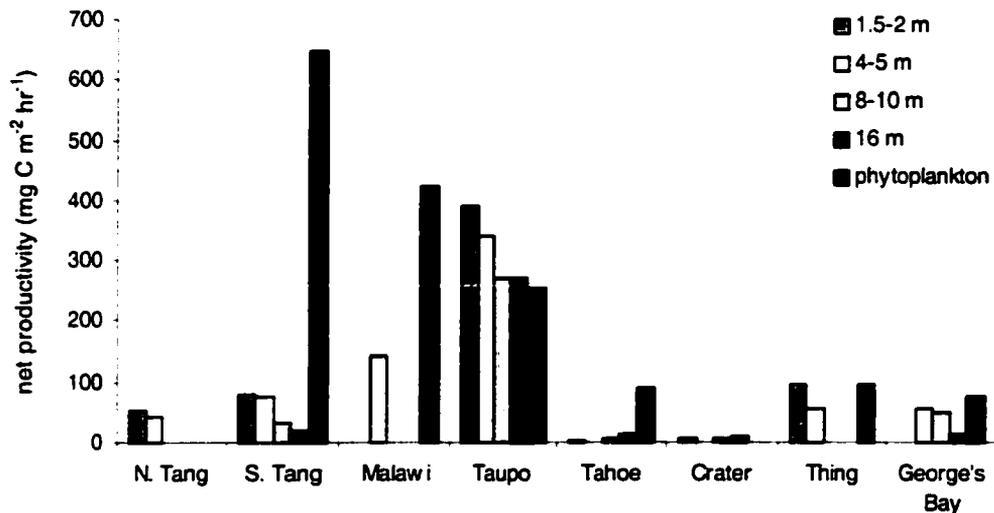


Figure C.3. A comparison of epilithic net productivity among large, oligotrophic lakes. Data for southern Lake Tanganyika (S. Tang.) are from this study. Sources (with abbreviations used in the figure) for the other data are as follows: North Tanganyika (N. Tang.) (Takamura 1988); Lake Malawi (Bootsma 1993); Lake Tahoe and Crater Lake, North America, (Loeb et al. 1982); Lake Taupo, New Zealand (Hawes and Smith 1994); Lake Thingvallavatn (Thing.), Iceland, (St. Jonsson 1992); George's Bay, Lake Huron, North America, (Duthie and Jones 1990). For phytoplankton data: Lake Tanganyika (Sarvala et al. 1999); Lake Malawi (Patterson and Kachinjika 1995); Lake Tahoe (Goldman 1988); Crater Lake (Loeb et al. 1982); Lake Taupo (Hawes and Smith 1994); Lake Thingvallavatn (Jonasson et al. 1992); George's Bay, (Duthie and Jones 1990).

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## **APPENDIX D: FOOD WEB STRUCTURE IN THE LITTORAL ZONE OF LAKE TANGANYIKA, EAST AFRICA: INSIGHTS FROM ISOTOPIC ANALYSES**

### **Abstract**

Identifying characteristics of stable food webs has been an important aspect of community ecology, particularly with respect to the role of broad dietary preferences relative to diet specificity in structuring food webs. In this study, we used stable carbon and nitrogen isotopes to determine primary carbon sources and energy flows in the littoral food web of Lake Tanganyika, East Africa. This littoral zone contains an extremely diverse fauna, and other studies have shown that fish community composition is stable and resilient. Carbon isotopes clearly distinguished between phytoplankton and benthic carbon. This allowed us to break the isotopic structure into three components: 1) species supported primarily by phytoplankton, 2) species supported by benthic carbon, and 3) species that must depend on a mix of benthic and pelagic carbon, either through a wide range in prey selection or detrital food sources. This study suggests that diet specificity is not important in diverse, stable food webs. Rather, broad dietary preferences may help stabilize the food web during environmental perturbations.

### **Introduction**

Since the early work of May (1972), there has been much debate over the structure required for stable food webs. Mathematical models suggest that species richness, food web complexity, and food chain length are important factors in determining the stability of ecological communities; stable model systems usually have fewer species, few trophic

levels, well-defined energetic pathways, and discrete trophic levels (Pimm 1982, Jordan and Molnar 1999). Omnivory (feeding on more than one trophic level) and broad dietary habits affect interaction strength and connectance, often leading to lower resilience and decreased stability (Pimm 1982). In contrast, empirical syntheses of food webs suggest that omnivorous feeding strategies (such as detritivory and cannibalism) are common, and that a more reticulate food web structure prevails in natural communities (Polis and Strong 1996).

The littoral food web in Lake Tanganyika, East Africa, provides an opportunity to examine the structure of a species-rich food web. The lake contains one of the world's most diverse freshwater faunas, and the littoral community is dominated by a cichlid species flock with high levels of endemism. Biological diversity is extremely high, with more than 200 fish species in the littoral zone (Coulter 1991). Long-term studies of this food web have revealed a persistent community composition among fishes, and removal experiments have shown high resilience, suggesting that this food web is fairly stable (Hori 1997). Given that this food web has high species richness, what structural components allow it to maintain stability? Specifically, does resource partitioning exert a strong influence on food web structure, with energy flows following discrete pathways? Or rather, is stability attained through broad, overlapping diets?

To date, studies of dietary habits among the littoral fish communities of Lake Tanganyika have been based on traditional methods of gut content analysis and observation. These cichlid species show a great divergence in jaw and tooth morphologies that correlates with supposed food preferences (Fryer and Iles 1972),

implying that diet specificity has been selected for and may play a pivotal role in food web structure. Diet specificity may also be important in driving evolution and maintaining co-existence of such high species richness, and food resource partitioning has been proposed as a mechanism for sympatric speciation in Lake Malawi, where similar large species flocks occur (Bootsma et al. 1996). So far the results are equivocal, with some studies promoting diet specificity (Brichard 1989) and others defining broad food-habit groups (Hori 1997).

We examined the role of food resource partitioning and diet specificity using stable isotopes to accurately trace energy flows paths in the Lake Tanganyika littoral food web. Carbon ( $^{13}\text{C}$ ) and nitrogen ( $^{15}\text{N}$ ) isotopes are useful in this regard, because they provide an unambiguous indicator of assimilated food energy (Michener and Schell 1994) and integrate diet over both time and space, thus removing an inherent problem in many food web studies (Pimm et al. 1991). Consumers reflect their diet with an average enrichment of 1‰ in  $^{13}\text{C}$  and 3.4‰ in  $^{15}\text{N}$  (Michener and Schell 1994). If food resource partitioning and diet specificity exist, a species will have isotopic ratios that are distinct from other species and there will be little variability within the species. However, if species have broad diets, isotope ratios will vary within a species and may overlap the isotopic ratios found in other species. Diet specificity should also create discrete trophic levels, which will be apparent as a step-wise enrichment in  $^{15}\text{N}$ . Omnivory will confound distinct trophic level enrichments because the isotope signal is integrated across more than one trophic level, and the overall enrichment will be less than the average trophic level enrichment of 3.4‰  $\delta^{15}\text{N}$ .

## **Methods**

The study was conducted at Jakobsen's Beach, just south of Kigoma, Tanzania. This location was relatively undisturbed, with no major sources of anthropogenic nutrient input, which has the potential to affect isotopic ratios by the introduction of terrestrial material that may be more enriched carbon and nitrogen isotopes. The site was well exposed to the lake and contained two small sandy beaches between rocky headlands. Prior fish surveys indicated that this area has a high diversity and density of cichlids (Darwall and Tierney 1998).

The nearshore community in Lake Tanganyika is fairly complex. Since we wanted to test diet specificity within a food web, we selected species whose diets are supposed to be restricted and sampled across several trophic levels. Our carbon source categories include phytoplankton, epilithic algae, loose material on rock surfaces (invertebrates and detritus) and sedimentary organic matter. Our consumer target species are thought to represent primary consumers (including epilithic grazers), secondary consumers, tertiary consumers, and detritivores, based on literature descriptions of their diet (Brichard, 1989).

### *Carbon sources - Primary producers and detritus*

A littoral food web has two potential primary energy sources – pelagic (open-water) phytoplankton or epilithon. These can be distinguished by their isotopic values, as epilithic algae have a more enriched carbon isotope than pelagic phytoplankton (France

1995, Hecky and Hesslein 1995). Phytoplankton were collected using vertical 10 m tows with a 50  $\mu\text{m}$  mesh net and were filtered through a 100  $\mu\text{m}$  mesh to remove zooplankton. Epilithic material (consisting of both algae and detritus) was collected using a syringe-scraper from rock tops at 2, 5, 7, 10, and 20 m. At 7 m, we distinguished among the loose material on the rock surface (detritus and invertebrates) and the actual epilithic algae growing on the rock top, sides, and bottom. The entire rock was 'vacuumed' with a handheld pump device, and the cleaned rock top, sides, and bottom were then scraped for algal material. For clarification, these vacuumed rock samples are referred to as epilithic algae, with the collected vacuum detritus (particles > 100 $\mu\text{m}$ ) referred to epilithic detritus, as distinguished from the unvacuumed samples which are referred to as epilithic material. All samples were collected on a 0.45  $\mu\text{m}$  glass-fiber filter and rinsed with 0.01N HCl and distilled water.

### *Invertebrates*

Zooplankton were caught using vertical tows with a 100  $\mu\text{m}$  mesh net. Zooplankton were placed in filtered lake water for 2 hours to clear gut contents and then collected on a 0.45  $\mu\text{m}$  glass-fiber filter and rinsed with 0.01N HCl and distilled water. Gastropod species (*Lavigeria grandis* and *Lavigeria coronata*) that are found in the gut of some cichlids were collected from rocks up to 2 m deep. The shell and digestive system were removed and the specimen was rinsed with distilled water. Crabs were obtained from fishermen, and although the exact provenance for these specimens is unknown, it is within the Kigoma area. We restricted our samples to the species *Platytelphusae armata*,

which is the most common crab species and is abundant in the rocky littoral zone (Coulter 1991). White muscle tissue was extracted from the carapace and rinsed.

### *Fish*

With such a diverse community, it is virtually impossible to acquire replicate samples for every fish species. We selected several species that are common in the littoral zone throughout the lake (Table 1). These species fall into a set of pre-defined food categories based on gut content analyses and observation (Brichard 1989, Hori 1997) – epilithic grazers, sediment sifters, zooplanktivores, and predators.

Fish were collected using gill nets set overnight at Jakobsen's Beach or were purchased from fishermen who had fished in the same locality using a net or line. White muscle tissue was taken from behind the dorsal fin, and in the case of specimens too small to obtain a sufficient muscle sample, the entire individual was used after removing the head, tail, and viscera.

All samples were dried at 50°C and stored wrapped in aluminum foil. Tissue samples were homogenized before analysis. Samples were analyzed at the University of Waterloo Environmental Isotope Lab on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carla Erba Elemental Analyzer (CHNS-O EA1108). Standard error is 0.2‰ for carbon and 0.3‰ for nitrogen. All isotope ratios are expressed in delta notation with respect to deviations from standard reference material (Pee Dee belemnite carbon and atmospheric nitrogen).

## Results

Average isotopic ratios for all food web samples are given in Table 1. Epilithic material showed a wide range of carbon and nitrogen isotopic ratios (Figure 1). Epilithic algae were significantly enriched in carbon compared to phytoplankton (z-test,  $z=397$ ,  $p<.0001$ ), and allows the food web to be broken into components supported by pelagic carbon, benthic carbon or a mix of these two (Figure 2). There were significant differences between carbon isotopes of algae on the tops, sides, and bottom of rocks (ANOVA,  $F=8.69$ ,  $p>.0035$ ). Carbon isotopes differed significantly between epilithic algae, epilithic detritus, and epilithic material (ANOVA,  $F=14.57$ ,  $p<.0001$ ), with epilithic algae most enriched and epilithic detritus the most depleted. There were also significant differences in  $^{15}\text{N}$  between epilithic algae, epilithic material, and epilithic detritus (ANOVA,  $F=13.96$ ,  $p<.0001$ ), with epilithic algae most depleted and epilithic material the most enriched. There were no significant differences in C:N ratios between these groups (ANOVA,  $F=2.24$ ,  $p<.12$ ).

In general, trophic level enrichments in  $^{15}\text{N}$  were lower than the expected value of  $3.4\text{‰}$  and decreased with increasing trophic level (Figure 3). Trophic level enrichment from the primary consumer level (mean  $\delta^{15}\text{N} = 2.79 \pm 2.63$ ) to the secondary consumer level (mean  $\delta^{15}\text{N} = 5.48 \pm 1.56$ ) averaged  $2.69\text{‰}$ . Enrichment between the secondary consumer level and the upper trophic level (mean  $\delta^{15}\text{N} = 5.85 \pm 0.76$ ) was only  $0.37\text{‰}$ .

## Discussion

### *Carbon sources - Primary producers and detritus*

The difference between benthic and pelagic productivity bases can be clearly distinguished using carbon isotope ratios, with benthic algae having much more enriched values. At these shallow water depths, epilithic algae has productivity rates several times that of planktonic algae (O'Reilly 1998), and isotopic values are enriched because carbon discrimination is low (Hecky and Hesslein 1995). Similar carbon isotopic ratios have been found for epilithic algae in other lakes, with values as enriched as  $-8\text{‰}$  in Lake Malawi (Hecky and Hesslein 1995, Bootsma et al. 1996). The depleted nitrogen isotopes reflect the importance of nitrogen fixation as a dominant nitrogen source for epilithic algae (Higgins 1999), and it is likely that epilithic algae throughout the lake have a  $\delta^{15}\text{N}$  close to  $0\text{‰}$ . Although the epilithic algae sampled in this study has been vacuumed, it is still possible that detritus or invertebrates were included in the sample, but in relatively small proportions that are unlikely to shift the isotopic signals significantly.

Epilithic detritus is the loose material on rock surfaces and is composed of planktonic particulates, invertebrates, fecal material from fishes, and other detrital matter. The relatively depleted carbon isotopes suggest that this detritus includes proportion of particulates derived from pelagic-based carbon. The enriched nitrogen isotopes imply the presence of heterotrophic material, and the highly enriched sample ( $\delta^{15}\text{N} = 9.69\text{‰}$ ) may also contain material of terrestrial origin, which has relatively enriched  $^{15}\text{N}$  ratios (Kendall 1998).

The more depleted carbon isotope signatures suggest that epilithic material contains pelagic-derived carbon and the relatively enriched nitrogen isotopes are consistent with heterotrophic material. Furthermore, it is unlikely that there is such a range in nitrogen source for benthic algae (-1.48‰ to 10.87‰), and these enriched values are consistent with detrital or other heterotrophic material. Clearly, isotopic food web studies should distinguish between epilithic algae and epilithic detritus.

*Primary consumers – benthic grazing species*

The grazing fish species are clearly supported by benthic carbon. As primary consumers, these species show an average  $\delta^{15}\text{N}$  enrichment of 3.5‰ relative to actual epilithic algae, which is similar to the average trophic enrichment of 3.4‰ (Minagawa and Wada 1984). However, in contrast to the grazing fishes, gastropods have a very small average trophic enrichment that is seen only relative to actual algae growing on rock tops. Low trophic enrichment between gastropods and epilithic algae has been recorded in other tropical and arctic lakes, where some gastropods also appeared depleted in  $^{15}\text{N}$  relative to bulk epilithion (Hecky and Hesslein 1995). An integrated algal sample, such as our epilithic scrapings, represents the average isotope values of the algal community and does not distinguish between algal and bacterial species. Gastropods may be species-selective in their food source and feed selectively on blue-green algae that rely heavily on nitrogen fixation and have more depleted  $\delta^{15}\text{N}$ .

### *Secondary consumers*

*Cyphotilapia frontosa*, *Lamprologus brichardi*, and *Cyprichromis* have similar carbon and nitrogen isotope values that indicate zooplankton as their food source. Behavioral patterns may contribute to niche partitioning through differential foraging, as these species consume zooplankton in spatially distinct locations in the water column (Brichard 1989). *L. brichardi* remain in a restricted range very near rock surfaces while *Cyprichromis* live in large schools up to tens of meters away from the rock surfaces and cover greater areas. *C. frontosa* exist between these two extremes, remaining within a few meters of the rock surfaces with moderate ranges.

*O. ventralis* and *L. sp. "Walter"* have isotopic ratios distinct from the other secondary consumers. Although previous work has suggested that these species feed on zooplankton (Brichard, 1989), their diet clearly includes a considerable proportion of benthic-based carbon. These isotope ratios are consistent with recent field observations that these species include benthic invertebrates in their diet (P. Verburg, pers. com.). The wide range of carbon and nitrogen isotopes within each species suggests that they are not specialist consumers.

Although three species in this nearshore food web are supposed to include gastropods in their diet, this is not reflected in their isotopic signals. Gut content analyses show a high proportion of gastropods in *Lobochilotes* (16%) and *Neolamprologus* (35%) relative to small fishes, invertebrates, ostracodes, and nematodes, with *Lavigeria grandis* as the dominant gastropod species (Cohen 1999). Clearly, the isotope values of these fish species suggest that, even though they are ingested, gastropods are not proportionally

assimilated. In southern Lake Tanganyika, *Lobochilotes* includes species of Ephemeroptera, Diptera and Trichoptera in its gut (Hori 1997), and insects may make up a greater proportion of assimilated carbon than formerly realized. *Lobochilotes* has also been described as a crab-eater (Brichard 1989), which is somewhat more consistent with the isotope structure of this littoral food web. However, the wide range of isotopic ratios for *Lobochilotes* and imply that this species has broad dietary habits. The other supposed gastropod-eater is the crab *Platyelphusae armata*, whose carbon isotopes suggest that it includes a large proportion of pelagic-based carbon in its diet rather than gastropod or benthic based carbon, and the relatively narrow range of its isotopic ratios ( $-19.4 \pm 0.18\text{‰} \delta^{13}\text{C}$  and  $5.0 \pm 0.26\text{‰} \delta^{15}\text{N}$ ) implies diet specificity in its food source.

*L. callipterus* and *Xenotilapia* sp. have been categorized as sifters or “engulfers” – species that ingest particulate matter such as sand and detritus while obtaining their prey (Yamaoka 1997). The main prey items for these species are probably shrimp and other benthic invertebrates that live on sandy bottoms. These fish species also have a wide range in isotopic ratios that reflects a generalist diet.

### *Tertiary consumers*

The depleted carbon ratios of the upper trophic level predatory fish species *B. microlepis* and *L. elongatus* imply these piscivores rely predominately on pelagic carbon. In contrast, the more enriched carbon values for the predator *L. lemariae* must include a proportion of benthic-based carbon. The trophic level  $^{15}\text{N}$  enrichment for these upper trophic levels is very low. This must be because other prey items with relatively depleted

$^{15}\text{N}$  make up a dominant proportion of their diet, implying that these predators are feeding on more than one trophic level and are omnivorous.

### *Food web structure*

The food web can be broken into components that are supported by either benthic or pelagic carbon or a mix of these two. The benthic component includes gastropods, grazing fishes and fish species that consume invertebrates such as ostracodes that live on rock surfaces (epilithic detritus). The pelagic component includes phytoplankton, zooplankton, the zooplanktivorous species, and some of the piscivores. This component exemplifies a classic food web with sequential carbon and nitrogen enrichment, as might be expected in aquatic systems (Polis and Strong 1996). However, many species lie between the two carbon end-member sources. These species rely neither on pelagic carbon nor benthic carbon but on must consume some combination of the two to acquire their intermediate carbon isotopic ratios. This intermediate carbon composition can be achieved either by a mix of benthic-based and pelagic-based prey or by relying on a detritus base. This suggests opportunistic feeding strategies rather than stenophagy, which is supported by the wide ranges in isotopic composition within a species.

Overall, the isotopic data suggest that this species-rich food web is structured by broad dietary preferences rather than selective resource partitioning and has a high potential for omnivory. First, the isotopic ratios often vary greatly within species at the secondary and tertiary consumer level, which is not consistent with diet specificity. Many species at the secondary and tertiary consumer level are generalist feeders.

Secondly, discrete trophic levels are non-existent. Fish species from primary consumers (epilithic grazers) to secondary consumers (zooplanktivores) and piscivores all fall within one trophic level with respect to their  $\delta^{15}\text{N}$  values. Low trophic enrichment at these upper trophic levels suggests that these piscivores may feed on more than one trophic level. Omnivory is generally thought to increase in prevalence with increasing trophic level (Polis and Strong 1996), and piscivores may conceivably be feeding on both primary and secondary consumer species or on detritus.

These broad dietary preferences may help stabilize the food web by allowing species to quickly adapt to changing environmental conditions. A specialized predator limited to particular prey items may not survive large fluctuations in prey abundance and has a greater time-to-recovery while mass accumulates up the food web after an initial increase in primary productivity. Omnivores can take dynamic shortcuts by taking advantage of increases or shifts in productivity by consuming lower trophic levels that respond more quickly to changes in primary productivity (Fagan 1997). Large lake level fluctuations in Lake Tanganyika (up to  $2 \text{ m year}^{-1}$ ) (Verburg et al. 1998) may cause sudden and dramatic shifts in the community structure and productivity of the benthos, for which upper trophic level species may compensate by having broad dietary preferences. The Lake Tanganyika littoral food web may be an example of how high species richness and connectance can increase resilience once stability has been achieved (Pimm 1982, Haydon 2000).

Table D.1. Isotope results for the littoral food web. The code corresponds to the symbols used for graphic representation of the data in subsequent figures. For habitat, additional information is as follows: OW – species that live in the open water column; RS– species that live within a meter of rock surfaces; RB– species that live within a few meters above rocky areas; RA– species that live in the open water above rocky areas; SA– species that live in the open water above sandy areas; SS– species that live within a meters of a sandy bottom. Food items were obtained from Brichard (1989). Values in parentheses indicate the number of samples for primary consumers or the number of replicates for a single sample for fish; n = 1 if no other value is given.

TABLE D.1. Isotope results for the littoral food web

| trophic level              | name                                   | code   | habitat              | food items            | $\delta^{13}\text{C}$ |               | $\delta^{15}\text{N}$ |               | C:N   |               |
|----------------------------|--|--------|----------------------|-----------------------|-----------------------|---------------|-----------------------|---------------|-------|---------------|
|                            |  |        |                      |                       | mean                  | std error (n) | mean                  | std error (n) | mean  | std error (n) |
| <b>primary producers</b>   |  |        |                      |                       |                       |               |                       |               |       |               |
|                            | phytoplankton                          | p      | OW                   |                       | -23.56                | 0.07 (6)      | 1.48                  | 0.08 (6)      | 7.44  | 0.24 (6)      |
|                            | epilithic algae                        | top    | 7 m top              |                       | -10.94                | 0.5 (9)       | 1.53                  | 1.88 (5)      | 9.94  | 0.65 (7)      |
|                            | epilithic algae                        | side   | 7 m side             |                       | -9.7                  | 0.7 (7)       | 1.05                  | 0.88 (7)      | 17.38 | 0.79 (7)      |
|                            | epilithic algae                        | bottom | bottom               |                       | -16.92                |               | -0.27                 |               | 11.85 |               |
|                            | epilithic material                     | 2      | 2 m                  |                       | -14.40                | 0.7 (5)       | 7.15                  | 1.76 (5)      | 16.81 | 1.12 (5)      |
|                            | epilithic material                     | 5      | 5 m                  |                       | -16.38                | 0.12 (4)      | 6.57                  | 0.77 (4)      | 9.97  | 0.53 (4)      |
|                            | epilithic material                     | 10     | 10 m                 |                       | -11.22                | 0.5 (4)       | 4.14                  | 0.5 (4)       | 15.13 | 0.1 (4)       |
|                            | epilithic material                     | 20     | 20 m                 |                       | -16.02                | 0.4 (5)       | 7.49                  | 0.61 (5)      | 8.43  | 0.34 (5)      |
| <b>detritus</b>            |  |        |                      |                       |                       |               |                       |               |       |               |
|                            | detritus                               | d      | rock surfaces at 7 m |                       | -13.23                | 0.81 (7)      | 3.65                  | 1.14 (7)      | 12.55 | 1.39 (7)      |
| <b>primary consumers</b>   |  |        |                      |                       |                       |               |                       |               |       |               |
|                            | zooplankton                            | z      | OW                   | phytoplankton         | -22.03                | 0.9 (4)       | 3.90                  | 0.17 (4)      | 4.64  | 0.14 (4)      |
| gastropods                 | <i>Lavigeria grandis</i>               | s      | RS                   | epilithon             | -11.91                |               | -0.44                 |               | 3.36  |               |
|                            | <i>Lavigeria grandis</i>               | s      | RS                   | epilithon             | -12.23                |               | 0.06                  |               | 3.63  |               |
|                            | <i>Lavigeria grandis</i>               | s      | RS                   | epilithon             | -12.98                |               | -0.17                 |               | 3.79  |               |
|                            | <i>Lavigeria grandis</i>               | s      | RS                   | epilithon             | -13.53                |               | -0.46                 |               | 3.37  |               |
|                            | <i>Lavigeria coronata</i>              | s      | RS                   | epilithon             | -14.19                |               | -0.81                 |               | 3.45  |               |
| fish                       | <i>Petrochromis</i> sp. 'Moshi yellow' | Pmy    | RB                   | epilithon             | -13.79                | 0 (2)         | 7.16                  | 0.1 (2)       | 3.02  | 0.1 (2)       |
|                            | <i>Petrochromis</i> sp. 'Moshi yellow' | Pmy    | RB                   | epilithon             | -13.04                |               | 3.32                  |               | 2.97  |               |
|                            | <i>Petrochromis</i> sp. 'Moshi yellow' | Pmy    | RB                   | epilithon             | -13.55                |               | 3.04                  |               | 2.91  |               |
|                            | <i>Petrochromis</i> sp.                | Psp    | RB                   | epilithon             | -13.52                |               | 2.98                  |               | 2.94  |               |
|                            | <i>Petrochromis</i> sp.                | Psp    | RB                   | epilithon             | -14.63                |               | 4.46                  |               | 3.20  |               |
|                            | <i>Tropheus duboisi</i>                | Td     | RB                   | epilithon             | -13.63                |               | 3.86                  |               | 2.95  |               |
|                            | <i>Tropheus duboisi</i>                | Td     | RB                   | epilithon             | -13.49                |               | 3.79                  |               | 2.94  |               |
| <b>secondary consumers</b> |  |        |                      |                       |                       |               |                       |               |       |               |
| fish                       | <i>Neolamprologus tetrocephalus</i>    | Nt     |                      | snails, invertebrates | -20.29                |               | 4.59                  |               | 2.95  |               |
|                            | <i>Lobochilotes labiatus</i>           | sLl    |                      | snails, invertebrates | -15.45                |               | 5.1                   |               | 2.99  |               |
|                            | <i>Lobochilotes labiatus</i>           | sLl    |                      | snails, invertebrates | -17.09                | 0.09 (2)      | 9.82                  | 0.28 (2)      | 3.16  | 0.005 (2)     |
|                            | <i>Lobochilotes labiatus</i>           | sLl    |                      | snails, invertebrates | -16.59                |               | 9.01                  |               | 3.08  |               |
|                            | <i>Cyprichromis</i> sp.                | Csp    | RA                   | zooplankton           | -20.71                |               | 5.55                  |               | 2.95  |               |
|                            | <i>Cyprichromis</i> sp.                | Csp    | RA                   | zooplankton           | -21.03                |               | 6.42                  |               | 3.19  |               |
|                            | <i>Cyprichromis</i> sp.                | Csp    | RA                   | zooplankton           | -20.78                |               | 5.21                  |               | 3.07  |               |
|                            | <i>Ophthalmotilapia ventralis</i>      | Ov     | RA                   | zooplankton           | -15.64                |               | 4.45                  |               | 3.43  |               |
|                            | <i>Ophthalmotilapia ventralis</i>      | Ov     | RA                   | zooplankton           | -14.97                |               | 4.07                  |               | 2.90  |               |
|                            | <i>Haplotaxodon microlepis</i>         | Hm     | OW                   | zooplankton           | -20.16                |               | 5.64                  |               | 3.01  |               |
|                            | <i>Haplotaxodon microlepis</i>         | Hm     | OW                   | zooplankton           | -20.43                |               | 5.6                   |               | 3.05  |               |

TABLE D.1, continued

|                      |                                     |    |    |                         |        |      |      |
|----------------------|-------------------------------------|----|----|-------------------------|--------|------|------|
|                      | <i>Lamprologus brichardi</i>        | Lb | RB | invertebrates on rocks  | -20.52 | 5.52 | 3.24 |
|                      | <i>Lamprologus brichardi</i>        | Lb | RB | invertebrates on rocks  | -21.18 | 5.12 | 3.30 |
|                      | <i>Cyphotilapia frontosa</i>        | Cf | RB | molluscs and fish       | -20.14 | 6.02 | 3.01 |
|                      | <i>Cyphotilapia frontosa</i>        | Cf | RB | molluscs and fish       | -20.15 | 5.87 | 3.06 |
|                      | <i>Lamprologus callipterus</i>      | Lc | SA | crustaceans, detritus   | -17.99 | 4.7  | 3.09 |
|                      | <i>Lamprologus callipterus</i>      | Lc | SA | crustaceans, detritus   | -19.33 | 4.53 | 3.12 |
|                      | <i>Lamprologus sp. 'Walter'</i>     | Lw | RB | zooplankton, ostracodes | -14.43 | 4.13 | 3.08 |
|                      | <i>Lamprologus sp. 'Walter'</i>     | Lw | RB | zooplankton, ostracodes | -16.66 | 4.9  | 3.04 |
|                      | <i>Lamprologus sp. 'Walter'</i>     | Lw | RB | zooplankton, ostracodes | -17.85 | 4.92 | 3.24 |
| <b>top predators</b> |                                     |    |    |                         |        |      |      |
| fish                 | <i>Lepidolamprologus elongatus</i>  | Le | RA | fish and shrimp         | -19.89 | 5.99 | 2.93 |
|                      | <i>Lepidolamprologus elongatus</i>  | Le | RA | fish and shrimp         | -18.39 | 4.18 | 2.88 |
|                      | <i>Lepidolamprologus elongatus</i>  | Le | RA | fish and shrimp         | -19.91 | 6.14 | 3.06 |
|                      | <i>Lamprologus lemariae</i>         | Li | RA | fish                    | -17.88 | 6.37 | 2.95 |
|                      | <i>Lamprologus lemariae</i>         | Li | RA | fish                    | -18.29 | 5.76 | 3.02 |
|                      | <i>Boulengerochromis microlepis</i> | Bm | OW | fish                    | -20.31 | 6.75 | 3.10 |
|                      | <i>Boulengerochromis microlepis</i> | Bm | OW | fish                    | -20.55 | 5.61 | 3.51 |
| <b>detritivores</b>  |                                     |    |    |                         |        |      |      |
| crabs                | <i>Platyelphusae armata</i>         | c  | RB | snails, detritus        | -18.97 | 4.78 | 3.06 |
|                      | <i>Platyelphusae armata</i>         | c  | RB | snails, detritus        | -19.24 | 5.79 | 3.02 |
|                      | <i>Platyelphusae armata</i>         | c  | RB | snails, detritus        | -19.71 | 4.78 | 3.22 |
|                      | <i>Platyelphusae armata</i>         | c  | RB | snails, detritus        | -19.67 | 4.68 | 3.24 |
| sand sifters         | <i>Xenotilapia sp.</i>              | X  | SS | detritus in sand        | -16.6  | 5.53 | 2.93 |
|                      | <i>Xenotilapia sp.</i>              | X  | SS | detritus in sand        | -18.39 | 4.18 | 2.88 |
|                      | <i>Xenotilapia sp.</i>              | X  | SS | detritus in sand        | -18.42 | 5.39 | 2.86 |

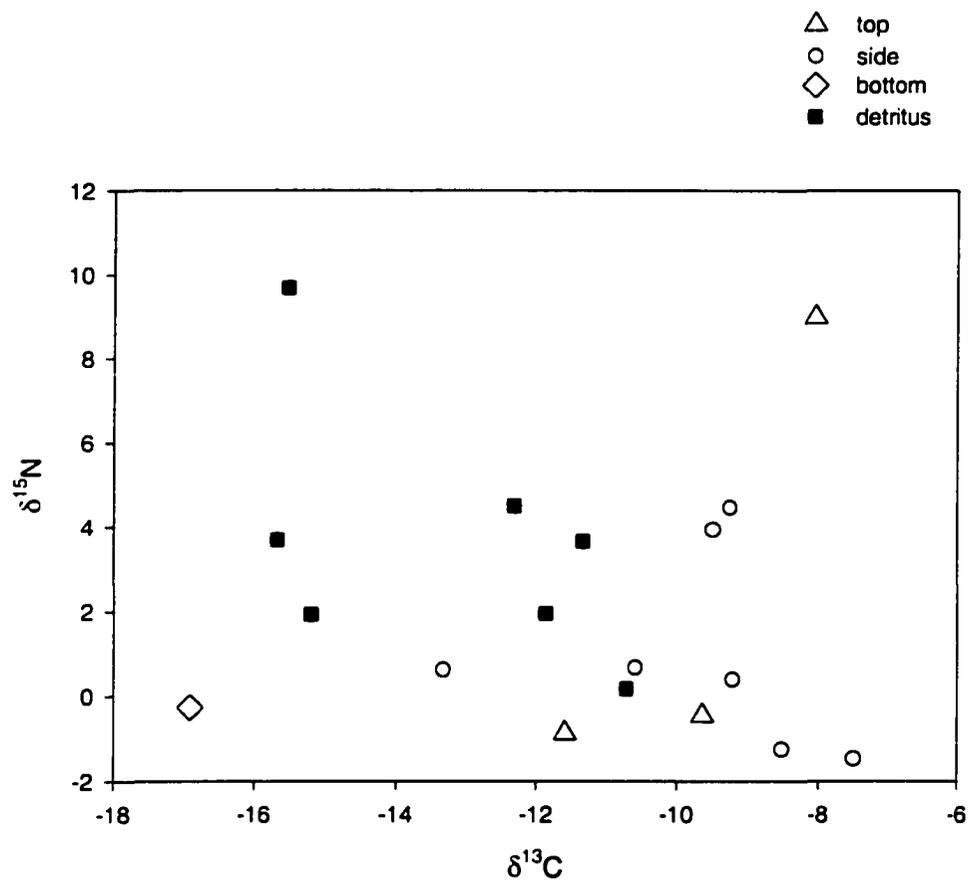


Figure D.1. Carbon and nitrogen isotopes for epilithic algal scrapings made after the rock was vacuumed to remove loose particles.

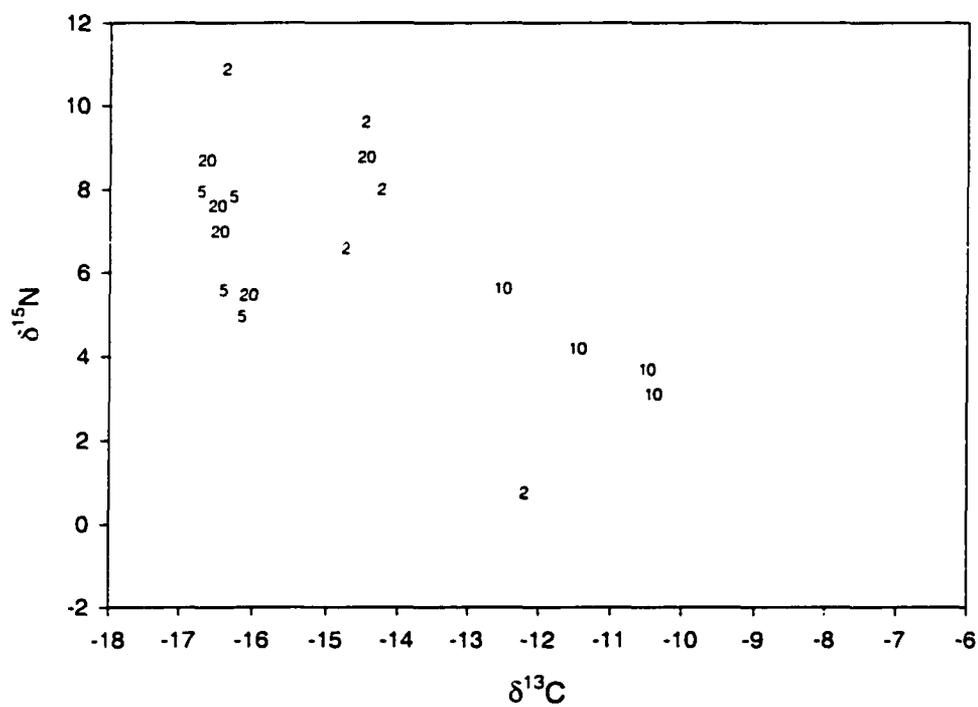


Figure D.2. Carbon and nitrogen isotopes for epilithic material. Each sample is represented by the depth at which it was collected. The axis scales are the same as Figure D. 1. for comparison.

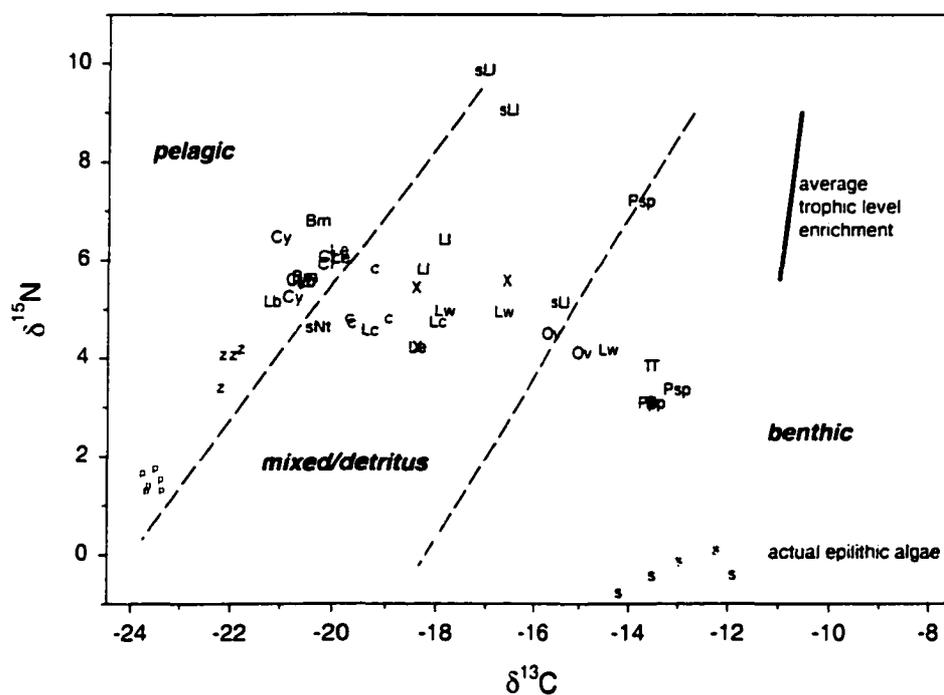


Figure D.3. Isotopic structure of the littoral food web. The code for the symbols can be found in Table D.1. The range of carbon and nitrogen isotopic ratios of actual epilithic algae is shown in the hatched area and the line in the upper right indicates the expected enrichment with trophic level increase. Lines delineating the pelagic, mixed, and benthic component were drawn based on species diet, such that all species known to be zooplanktivores or epilithic grazers were placed in their respective component.

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**APPENDIX E: INTERPRETING STABLE ISOTOPES IN FOOD WEBS:  
RECOGNIZING THE ROLE OF TIME-AVERAGING AT DIFFERENT  
TROPHIC LEVELS**

Interpreting stable isotopes in food webs: Recognizing the role of time-averaging at different trophic levels.

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*Abstract* – Lake Tanganyika, East Africa, has a simple pelagic food chain, and trophic relationships have been established previously from gut content analysis. Instead of expected isotopic enrichment from phytoplankton to upper level consumers there was a depletion of  $^{15}\text{N}$  in August 1999. The isotope signatures of the lower trophic levels were an indicator of a recent upwelling event, identified by wind speed and nitrate concentration data, that occurred over a 4 day period several days prior to sampling. The isotope structure of the food web suggests that upwelled nitrate is a nutrient source rapidly consumed by phytoplankton but the distinctive signature of this nitrate is diluted by time-averaging in the upper trophic levels. This time-averaging is a consequence of the fact that the isotopic signature of an organism is related to variable nitrogen sources used throughout the life of the organism. This study illustrates the importance of recognizing differences in time-averaging among trophic levels.

*Introduction* – Stable isotopes are becoming a standard analytical tool in food web ecology. Differences in carbon and nitrogen isotope ratios between consumers and their diet provide information on energy flows, nutrient sources, and trophic relationships. Typically, carbon provides information on the primary energy source (e.g. benthic vs. pelagic photosynthesis), while nitrogen allows discrimination among trophic levels. Relative enrichment with increasing trophic level often allows a better interpretation of dietary relationships than gut content analysis alone because isotope ratios record material that is actually assimilated (Michener and Schell 1994). Recent field studies have shown an average enrichment of  $0.05\text{‰} \pm 0.63 \delta^{13}\text{C}$  and  $3.49\text{‰} \pm 0.23 \delta^{15}\text{N}$  (Zanden and Rasmussen in press) and are similar to the commonly used trophic fractionation values of  $1\text{‰} \delta^{13}\text{C}$  and  $3.4\text{‰} \delta^{15}\text{N}$  (Michener and Schell 1994). The ease of stable isotope analyses makes them an appealing tool in ecology, but care must be taken in interpretation of the results (Gannes et al. 1997). An isotopic ratio of an organism is usually understood to represent its diet, but it should be remembered that this isotopic ratio is also time-specific, representing an average ratio related to tissue turnover rate and the life of the organism.

The pelagic food web in Lake Tanganyika, East Africa, provided an excellent example of how stable isotopic analyses may not be straightforward. Lake Tanganyika is a deep (mean 570 m; max 1470 m), large (mean width 50 km; length 650 km) lake located a few degrees south of the equator. The lake is permanently stratified and is anoxic below approx. 150 m. Lake Tanganyika has a simple pelagic food web, and trophic relationships have been established previously from gut content analysis (Fig.

1)(Coulter 1991). The zooplankton are dominated by the copepod *Tropodiaptomus simplex*, a major dietary component of the two clupeid fish species, *Stolothrissa tanganicae* and *Limnothrissa miodon*. The upper trophic level is represented by four *Lates* species. Of these, *Lates angustifrons* and *Lates mariae* rely on nearshore fishes as a food source throughout their lives. *Lates microlepis* spend their larval and juvenile stages near shore and recruit to the pelagic as adults, whereas *Lates stappersi* has a fully pelagic life cycle. Thus, the most abundant species of the pelagic food web form a linear food 'chain' from phytoplankton to the copepod *T. simplex* to the zooplanktivorous *Stolothrissa* to the predatory *L. stappersi*. This linear food chain should be apparent as a distinct sequential enrichment in the carbon and nitrogen isotopes with increasing trophic level (Michener and Schell 1994).

*Methods* – Our study took place near Kigoma, Tanzania, during the dry season. Food web samples were collected approximately 15 km offshore (4° 50' S, 29° 29' E) during the night of August 1, 1999. Phytoplankton were collected using vertical tows with a 50 µm mesh net (n = 6). Samples were filtered through 100 µm mesh to remove zooplankton, then collected on 0.45 µm glass-fiber filters and rinsed with 0.01N HCl and distilled water. Zooplankton were caught using vertical tows with a 100 µm mesh net (n = 4). They were placed in filtered lake water for 2 hours to clear gut contents, then collected on 0.45 µm glass-fiber filters and rinsed with 0.01N HCl and distilled water. Fish specimens of *Stolothrissa* (n = 6), *Limnothrissa* (n = 5), *Lates stappersi* juveniles (n = 4), and *Lates stappersi* (n = 4) were obtained from local fishermen who were fishing

adjacent to the site when the plankton samples were collected. For all species except *Stolothrissa*, we collected a section of white muscle tissue from behind the dorsal fin. As *Stolothrissa* were too small to obtain a large muscle sample, we used the entire body after removing the head, tail, and viscera. Fish samples were washed with distilled water, dried, and homogenized before analysis. All samples were dried at 50°C and stored wrapped in aluminum foil.

Samples were analyzed at the University of Waterloo Environmental Isotope Lab on an Isochrom Continuous Flow Stable Isotope Mass Spectrometer (Micromass) coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108). The isotope ratios are expressed in delta notation with respect to deviations from standard reference material (Pee Dee belemnite carbon and atmospheric nitrogen). Standard error is 0.2‰ for carbon and 0.3‰ for nitrogen. Statistical analyses were done using JMP IN (SAS Institute, Inc.)

*Isotope structure of the food web* – Overall, the isotope structure of the pelagic food web was not that of a linear food chain (Fig 2). There was a general trend of carbon enrichment but a depletion of nitrogen with trophic level increase. The enrichment in  $\delta^{13}\text{C}$  across the lower food web from phytoplankton to *Stolothrissa* was larger than would be predicted. We expected a total  $\delta^{13}\text{C}$  enrichment of 2‰ across two trophic levels (Michener and Schell 1994), while the enrichment here was 4‰. Furthermore, the  $\delta^{15}\text{N}$  ratios did not show the expected 3.4‰ enrichment with increasing trophic level.

*The upper food web* – For the upper pelagic food web, isotopic analyses were consistent with the expected diet specificity in these fish species. The primary prey item for adult *L. stappersi* is *Stolothrissa*, and this relationship was clearly seen in the isotope data, where *L. stappersi* was approximately 1‰ enriched in  $^{13}\text{C}$  and 2‰ enriched in  $\delta^{15}\text{N}$  relative to *Stolothrissa*. Juvenile *L. stappersi* were significantly depleted in  $\delta^{15}\text{N}$  compared to the adults (one-sided *t*-test,  $p < 0.02$ ), which reflects the fact that their diet includes relatively more copepods (Mannini et al. 1999). The other clupeid species, *Limnothrissa*, includes smaller *Stolothrissa* in its diet, which is likely the reason for its isotopic enrichment relative to *Stolothrissa*.

*A recent change in the nutrient source* – We used the isotopic ratios of the fish species and established isotopic relationships between trophic levels to predict isotope values for the primary energy source (Fig 2). Both zooplankton and phytoplankton are depleted in  $\delta^{13}\text{C}$  compared to predicted ratios. Given the  $\delta^{15}\text{N}$  values of the upper food web and likely importance of atmospheric N fixation in Lake Tanganyika (Hecky 1991), we predicted phytoplankton would have a  $\delta^{15}\text{N}$  value near 0‰. Instead, phytoplankton had a  $\delta^{15}\text{N}$  of between 6 and 8‰, similar to that of zooplankton and slightly enriched compared to the upper consumer levels. A discrepancy of this magnitude cannot be explained easily by either a change in phytoplankton productivity rates or species composition and thus implies a change in nitrogen source.

Although the primary sources of new nitrogen are atmospheric deposition and biological nitrogen fixation, internal loading of deep-water nutrients is also an important nutrient source for the pelagic zone (Hecky et al. 1991). Lake Tanganyika is permanently stratified, but strong winds during the dry season cause seiche activity with a 28 to 36 day period, leading to episodic vertical metalimnion entrainment (Plisnier et al. 1999). Wind speeds vary diurnally, but daily mean speeds were significantly higher in the week preceding sampling ( $1.48 \pm 0.09 \text{ m s}^{-1}$ ) than in the week following sampling ( $0.81 \pm 0.08 \text{ m s}^{-1}$ ), with four consecutive days where speeds were higher than the long-term seasonal mean (Johannes et al. 1999). Concurrently, nitrate concentration profiles showed upwelling of nitrate from 100 m deep around 28 July (Fig. 3) (Johannes et al. 1999). These data provide strong evidence that an upwelling event occurred four to six days prior to sampling the food web.

This deep-water nitrogen is likely enriched in  $^{15}\text{N}$  (Francois et al. 1996). The metalimnion of Lake Tanganyika has low oxygen levels and elevated nitrate concentrations (Hecky et al. 1991). As denitrification occurs in the suboxic section of the water column, the lighter isotope is selectively removed, and the remaining nitrate becomes increasingly enriched in  $^{15}\text{N}$ . Field studies in temperate lakes have shown that fractionation during nitrogen assimilation by phytoplankton can be  $-4$  to  $-5\text{‰}$  if nitrogen is in excess (Fogel and Cifuentes 1993), which implies that the nitrogen source for these phytoplankton would require a  $\delta^{15}\text{N}$  of at least 10 to 14‰. Denitrification has fractionations in the range of 10 to 30‰ (Wada and Hattori 1991), which would lead to an enriched nitrate pool in the suboxic metalimnion of Lake Tanganyika. For other lakes,

investigators have measured deep-water nitrate values of 15.1‰ (Yoshioka et al. 1988) or have calculated values between 10 to 30‰ (Teranes and Bernasconi 2000).

A short-term, episodic nutrient input from deeper water to the epilimnion would alter phytoplankton isotopic signals, eventually causing them to have  $\delta^{15}\text{N}$  signatures in the range observed in this study. With high nitrate concentrations, discrimination against the heavier nitrogen isotope occurs and initially phytoplankton are depleted relative to dissolved nitrogen. Following Rayleigh fractionation kinetics, the remaining nitrate becomes relatively enriched. As the algal bloom continues, however, demand for nitrogen remains high and discrimination against the heavier isotope decreases as nitrogen concentrations decline. The pelagic zone of Lake Tanganyika is usually nitrogen limited (Hecky et al. 1991), implying that Rayleigh fractionation continues to near-completion. Thus, phytoplankton eventually attain an isotope value similar to that of their nitrogen source.

Supporting evidence that phytoplankton were recording upwelling in their nitrogen isotopic ratios existed in their carbon isotope signal. Under conditions of high nutrient availability, phytoplankton productivity increases and discrimination against the heavier carbon isotope eventually decreases, giving them an enriched carbon signal (Farquhar et al. 1989). The fact that the phytoplankton signal in Lake Tanganyika was relatively depleted after upwelling indicates a source of depleted dissolved inorganic carbon (DIC). In general, deep-water DIC is depleted relative to surface DIC through dissolution and oxidation of carbonate and organic carbon. Craig (1974) found that metalimnetic DIC in Lake Tanganyika was depleted by 1.5‰ relative to surface water. Uptake of this

upwelled DIC by phytoplankton would cause them to have a  $\delta^{13}\text{C}$  value that was depleted compared to average conditions.

Time-averaging explains the lack of trophic enrichment with respect to  $\delta^{15}\text{N}$  and the large  $\delta^{13}\text{C}$  enrichment ( $2\text{‰}$ ) between the lower trophic levels. This straightforward food chain has different turnover times associated with each trophic level. Phytoplankton population growth rates are  $1.2 \text{ day}^{-1}$  or higher (Hecky 1991), and thus their stable isotope signal represents carbon and nitrogen uptake and sources over the last few days.

Preliminary evidence suggests that the time to full development for copepods in Lake Tanganyika is 31 to 45 days (Hyvonen 1997); thus their isotopic ratios represent an average of phytoplankton consumed both pre- and post-upwelling. The clupeid *Stolothrissa* integrates diet over a period of several months to one year, and the predatory *L. stappersi* has a life span of several years (Coulter 1991). The effect of this greater temporal integration is seen in the upper food web in Lake Tanganyika, where the short-term fluctuation in nutrient source is not apparent. Time-averaging of this type has been invoked in Lake Ontario, where the isotopic signature of late summer zooplankton may be reflecting phytoplankton consumed earlier in the summer (Leggett et al. 1999).

In summary, this study illustrates the importance of understanding the temporal resolution of different trophic levels and the effect of time-averaging in stable isotope ecology. Isotopic signals of primary producers are subject to greater variation than other trophic levels in this system because of constantly changing nutrient sources and concentrations. It is precisely because of this variation that food web modeling using isotopes is usually based on the isotope signal of the primary consumer, whose longer-

term integration is assumed to reduce the short-term variability found in primary producers (i.e. Post et al. 2000). However, this work suggests that temporal variation may be significant at the primary consumer level and could affect assessment of relative trophic level. Temporal integration must be considered when comparing organisms whose isotopic compositions average over different time scales.

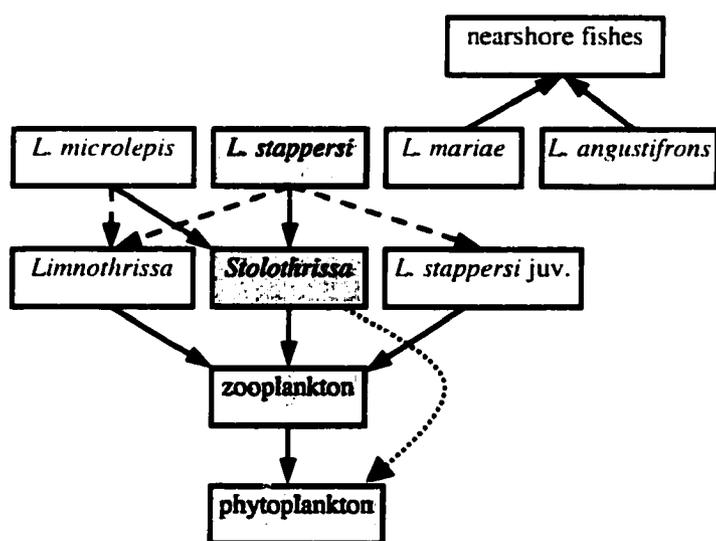


Figure E.1. The pelagic food web of Lake Tanganyika. The solid lines indicate major food preferences; the dashed lines indicate other prey relationships. *Lates mariae* and *Lates angustifrons* also include a minor proportion of *Stolothrissa tanganyicae* and *Limnothrissa miodon* among their prey. The shaded boxes represent the dominant species of the pelagic zone and illustrate the linear food chain relationship. Modified from Coulter (1991).

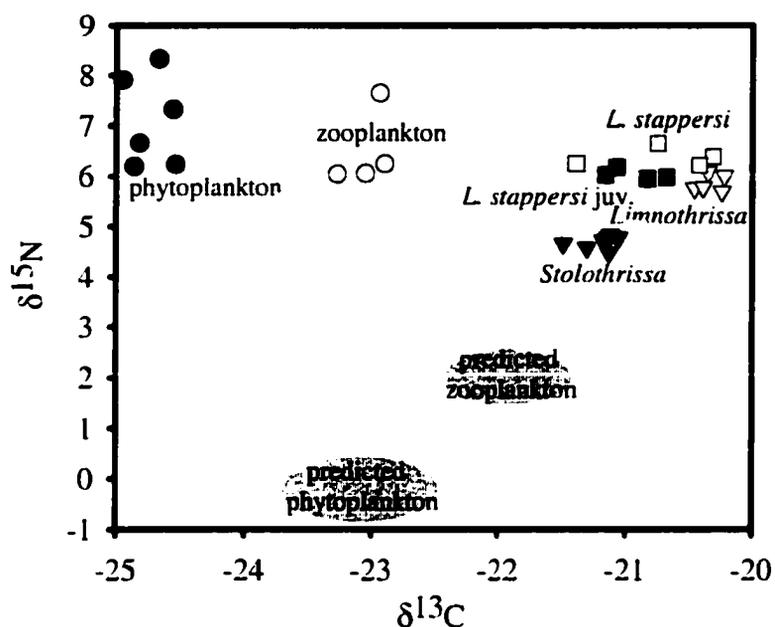


Figure E.2. The isotope structure of the pelagic food web. Each data point represents an individual organism. Predicted values for zooplankton and phytoplankton are based on isotopic values of the upper food web using standard trophic enrichments ( $1\text{‰}$   $\delta^{13}\text{C}$  and  $3.4\text{‰}$   $\delta^{15}\text{N}$ ) and the enrichments seen in the upper food web ( $1\text{‰}$   $\delta^{13}\text{C}$  and  $2\text{‰}$   $\delta^{15}\text{N}$ ). Closed circles are phytoplankton, open circles are zooplankton, solid triangles are *Stolothrissa*, open triangles are *Limnothrissa*, solid squares are *Lates stappersi* juveniles, and open squares are *L. stappersi* adults.

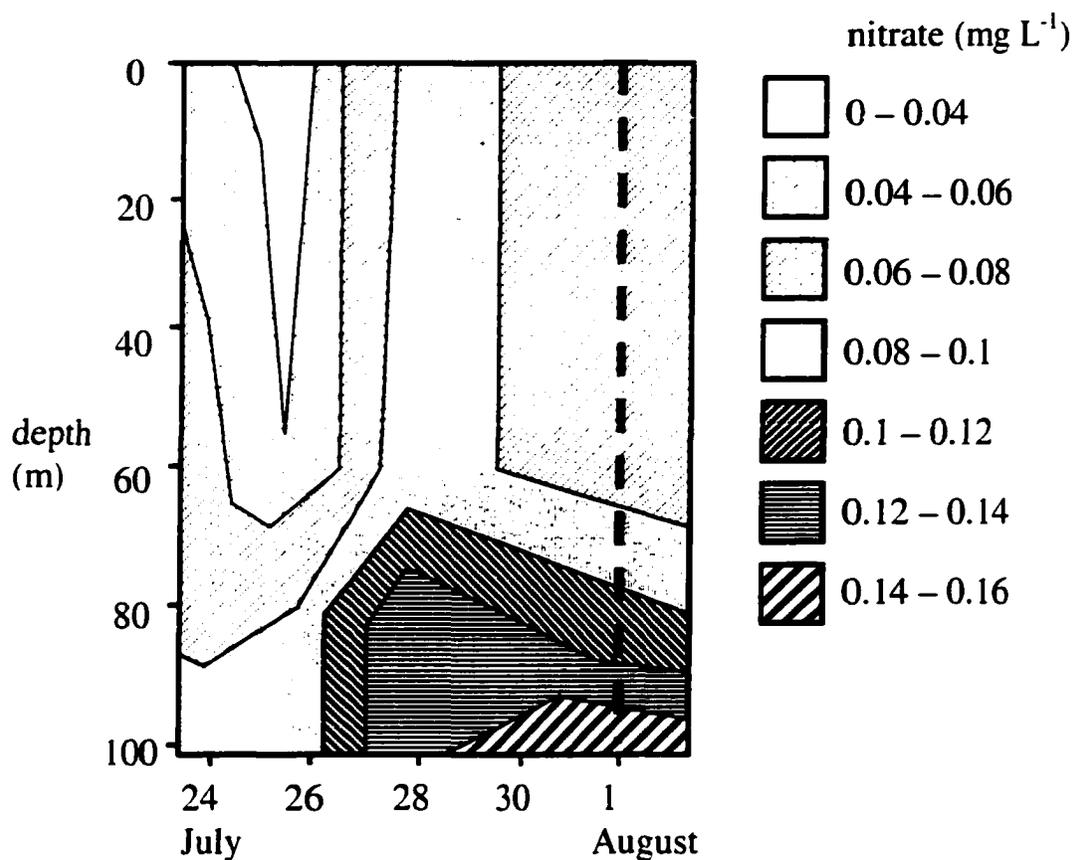


Figure E.3. Nitrate concentration profiles. Nitrate concentrations from surface waters to the upper metalimnion off Kigoma Bay throughout the week prior to sampling. The dashed line indicates the sampling date. Upwelling of water from 100 m deep is indicated by the increase in nitrate concentrations around 28 July. Data from Johannes et al. (1999).

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Table 1. Carbon and nitrogen isotopes for the pelagic food web.

| trophic level              | species name                   | $\delta^{13}\text{C}$ | $\delta^{15}\text{N}$ | C:N  |
|----------------------------|--------------------------------|-----------------------|-----------------------|------|
| <b>primary producers</b>   |                                |                       |                       |      |
|                            | phytoplankton                  | -24.67                | 8.33                  | 7.14 |
|                            | phytoplankton                  | -24.82                | 6.66                  | 6.82 |
|                            | phytoplankton                  | -24.56                | 7.31                  | 6.84 |
|                            | phytoplankton                  | -24.95                | 7.91                  | 8.15 |
|                            | phytoplankton                  | -24.66                | 6.19                  | 7.71 |
|                            | phytoplankton                  | -24.54                | 6.23                  | 8.00 |
| <b>primary consumers</b>   |                                |                       |                       |      |
|                            | zooplankton                    | -22.9                 | 6.24                  | 4.40 |
|                            | zooplankton                    | -23.27                | 6.04                  | 4.75 |
|                            | zooplankton                    | -22.94                | 7.64                  | 4.18 |
|                            | zooplankton                    | -23.05                | 6.05                  | 4.44 |
| <b>secondary consumers</b> |                                |                       |                       |      |
|                            | <i>Stolothrissa tanganicae</i> | -21.13                | 4.48                  | 3.24 |
|                            | <i>Stolothrissa tanganicae</i> | -21.06                | 4.78                  | 3.23 |
|                            | <i>Stolothrissa tanganicae</i> | -21.18                | 4.73                  | 3.23 |
|                            | <i>Stolothrissa tanganicae</i> | -21.12                | 4.83                  | 3.30 |
|                            | <i>Stolothrissa tanganicae</i> | -21.49                | 4.66                  | 3.19 |
|                            | <i>Stolothrissa tanganicae</i> | -21.31                | 4.58                  | 3.25 |
|                            | <i>Stolothrissa tanganicae</i> | -21.14                | 4.78                  | 3.19 |
|                            | <i>Limnothrissa miodon</i>     | -20.46                | 5.76                  | 3.00 |
|                            | <i>Limnothrissa miodon</i>     | -20.39                | 5.78                  | 3.03 |
|                            | <i>Limnothrissa miodon</i>     | -20.35                | 6.08                  | 3.00 |
|                            | <i>Limnothrissa miodon</i>     | -20.22                | 6                     | 3.05 |
|                            | <i>Limnothrissa miodon</i>     | -20.24                | 5.69                  | 3.00 |
| <b>top predators</b>       |                                |                       |                       |      |
|                            | <i>Lates microlepis</i> juv.   | -20.44                | 6.05                  | 2.96 |
|                            | <i>Lates stappersi</i> juv.    | -21.16                | 6.02                  | 3.56 |
|                            | <i>Lates stappersi</i> juv.    | -20.83                | 5.95                  | 3.49 |
|                            | <i>Lates stappersi</i> juv.    | -20.68                | 5.98                  | 3.32 |
|                            | <i>Lates stappersi</i> juv.    | -21.07                | 6.17                  | 3.53 |
|                            | <i>Lates stappersi</i>         | -20.75                | 6.65                  | 3.38 |
|                            | <i>Lates stappersi</i>         | -20.31                | 6.38                  | 3.07 |
|                            | <i>Lates stappersi</i>         | -21.39                | 6.25                  | 3.72 |
|                            | <i>Lates stappersi</i>         | -20.42                | 6.21                  | 3.23 |
|                            | <i>Lates augustifrons</i>      | -21.66                | 8.04                  | 4.03 |