Algal quality controls the distribution, behavior and growth of algivorous cichlids in Lake Tanganyika

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By

Renalda N. Munubi

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I HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER MY SUPERVISION BY Renalda N. Munubi ENTITLED Algal quality controls the distribution, behavior and growth of algivorous cichlids in Lake Tanganyika, BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF Doctor of Philosophy.

_____

Yvonne Vadeboncoeur, Ph.D.
Dissertation Director

_____

Donald Cipollini, Ph.D.
Director, ES Ph.D. Program

_____

Robert E.W. Fyffe, Ph.D.
VP for Research and
Dean of the Graduate School

Committee on Final Examination

_____

Peter B. McIntyre, Ph.D.

_____

Rashid Tamatamah, Ph.D.

_____

Jeffrey Peters, Ph.D.

_____

Lynn Hartzler, Ph.D

ABSTRACT

Munubi N., Renalda Ph.D., Environmental Sciences Ph.D. Program, Wright State University, 2015. Algal quality controls the distribution, behavior and growth of algivorous cichlids in Lake Tanganyika.

The nutritional value of primary producer is dependent on the concentrations of C, N and P. These elements are the building blocks for protein, carbohydrates, lipids, nucleic acids and other biochemical compounds. The balance between the supply of dietary elements and the herbivore's demand is crucial for the growth of algivorous organisms, including fish. However, anthropogenic changes in primary producer quality due to sediments may alter the value and quantity of food in the littoral zone of Lake Tanganyika, which may affect both herbivorous near shore and pelagic fisheries. This dissertation focuses on the influence of algae food on herbivore fish.

First, I explored the influence of algal quality and quantity on fish growth rates. I fed fish food with different phosphorus concentrations at high and low ration. I found that the growth rate of *T.moorii* was strongly influenced by the combination of food quality and quantity only when fish were fed good quality food. Lower food quality reduced specific growth rates. When fish are fed poor food, there was no compensation by simply increasing the quantity.

I also examined how algal quality and quantity varies among site, and how fish changes their feeding behavior based of food availability. I found that herbivore can

potentially practice selective feeding, physiological and morphological adaptations in order to adjust to differences food quality and quantity.

Lastly, I examined the relationship between algal resources, fish density and condition factor among and within sites along depth gradient from 1 to 8 m. I found that within sites, fish density, periphyton quality and quantity all decreased with depth, a pattern consistent with fish maximizing energy and nutrient input by aggregating in shallow areas. Among sites, the distribution of algivores was positively correlated with food quality and negatively correlated with algal biomass, patterns that indicate a strong bottom-up and top-down effects of fish on algae.

Terms used and abbreviation

C	Carbon
N	Nitrogen
P	Phosphorus
C: P	Carbon to phosphorus ratio (molar)
N: P	Nitrogen to phosphorus ratio (molar)
C: N	Carbon to nitrogen ratio (molar)
FA	Fatty acid
PUFA	Polyunsaturated fatty acid •
ARA	Arachidonic acid, 20:4w6
DHA	Docosahexaenoic acid, 22:6w3
EPA	Eicosapentaenoic acid, 20:5w3
SAFA	Saturates Fatty Acids
RNA	Ribonucleic acid
DGR	Daily growth rates
Bottom-up control"	refers to "control of algal biomass by nutrient supply via algal growth,"
Top-down control"	refers to "control of algal biomass by grazing via algal removal.

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DEDICATION

This dissertation is dedicated to my children Grant Misinzo and Jonathan Misinzo, whose unyielding love, support, and encouragement has enriched my soul and inspired to complete this research.

Introduction

Lake Tanganyika is situated within the Albertine rift valley and is bordered by four countries (Burundi, Democratic Republic of Congo, Tanzania and Zambia). Lake Tanganyika holds one sixth of the world's fresh water (Naithani et al., 2011) and is the world's longest freshwater lake, and is second only to Lake Baikal in depth and volume (Coulter, 1991). Its average depth is 570 m and its maximum depth is 1,470 m. Lake Tanganyika supports the most productive freshwater pelagic fishery of the four bordered countries making it an important regional source of protein (Mölsä et al., 1999). It is also used for transportation, communication and source of potable water (Coulter, 1991; Nkotagu, 2008).

The lake has remarkable fish diversity with an estimated 250 morphologically and behaviorally diverse cichlid fish species that mainly inhabit the lake's littoral habitats (Rossiter, 1995). Most of the fish in the rocky littoral zone of Lake Tanganyika are algivorous cichlids that graze on algae that are attached on the rocky shore habitat of the littoral zone (Yanagisawa and Nishida, 1991; Brichard, 1989; Rossiter, 1995). Cichlid fishes of the *Tropheus* and *Petrochromis* genera are the dominant algivorous fish species distributed throughout all the rocky shore habitats where periphyton is abundant with high productivity (Hori et al., 1983).

Lake Tanganyika is currently confronted by a number of threats including the degradation of its watershed (Alin et al*.,* 2002) and global climate change (Kraemer et al., 2015; O'Reilly et al*.,* 2003; Verburg et al., 2003). Both threats are already impacting the

function of the lake resulting in a reduction of fishery productivity (Stenuite et al., 2007; Donohue and Molinos, 2009), primary productivity (Heckyet al., 1981; O'Reilly et al., 2003) and nutrient availability. The decline in primary productivity may affect both near shore and pelagic fisheries since the Lake Tanganyika food web is based on algal productivity (Sumaila et al., 2011).

Over the last century, Lake Tanganyika's surface and deep water temperatures have risen (Verburg et al., 2003; O'Reilly et al., 2003). In addition, wind velocities in the Lake Tanganyika watershed have declined by 30% since the late 1970's (O'Reilly et al., 2003; Corman et al., 2010). The increased air and surface water temperatures and decreased wind velocity have increased thermal stratification and stability of the water column resulting in reduced frequency and magnitude of nutrient upwelling (Kraemer et al., 2015; O'Reilly et al., 2003; Verburg et al., 2003). Furthermore, reduced strength and frequency of upwelling decreases the availability of nutrients from the deep-water nutrient reservoir to the surface that are essential for primary production (O'Reilly et al., 2003).

Lake Tanganyika catchment area is inhabited by a rapidly growing human population of about 10 million mainly practicing small scale agricultural activities for their livelihood (Nkotagu, 2008). Anthropogenic and economic activities in the catchment area have resulted in deforestation leading to higher erosion rates and sediment loading into Lake Tanganyika. Increased sediment runoff during the rainy season can lead to sediment accumulation on near shore rocks (Lloyd et al., 1987; Dettman et al.,

2005). Sediments can cover benthic algae, potentially reducing its nutritional value (Donohue and Molinos, 2008), and consequently decreasing the foraging efficiency of algivorous fish (Cohen et al., 1993). Increases in sedimentation also reduce habitat complexity by filling crevices and other sheltered areas among rocks that are important as hiding, breeding and feeding sites for fish (Donohue and Irvine, 2004; Takamura, 1984). Sediments also increase turbidity of the water column reducing visibility for the fish, as well as light penetration to periphyton (Vadeboncoeur and Steinman, 2002; McIntyre et al., 2005; Nkotagu, 2008). Accordingly, high levels of sediments may induce mortality in larvae and juvenile stages because small fish has a relatively high oxygen demand per unit body weight. Small sized gills may entraps suspended partials easily thus interferes with gaseous exchange (Bunt et al., 2004).

Algivorous cichlid fish are primary consumers that feed on benthic algal assemblage and form an important link in the food chain by providing nutrient and energy to higher organisms in the trophic levels. However, anthropogenic activities and climate change in Lake Tanganyika have the potential to alter both the quality and the quantity of periphyton. Characterizing this relationship may be critical to understanding the processes by which environmental change can affect the distribution, behavior, and growth of algivorous cichlids.

Chapter one of this dissertation assess the influence of food nutritional quality (C:N:P) and quantity (ration either high or low amount of food) on the growth and excretion of the algivorous fish (*Tropheus Brichardi*). The diets of primary consumers

are of poor quality, rich in carbon relative to nitrogen and phosphorus (Sterner and Elser, 2002). The C to P ratio of periphyon is higher and more variable than that of herbivores (Sterner and Hessen, 1994). Hence due to the relatively low nutrient concentrations of a plant-based diet, herbivores' growth can be limited by the intake of phosphorus rather than energy (Sterner and Hessen, 1994).

In Chapter Two, I examine how periphyton nutritional quality, quantity and sediments affect fish feeding behavior. Climate change and anthropogenic activities decrease both nutritional quality and quantity. This decrease may negatively affect the growth rate of herbivores since the amount of energy and nutrients acquired per unit time are determined by both the time allocated for foraging activities (Abrams, 1984), and the quality and quantity of food. However, algivores including *T.brichardi* can modify their feeding behavior and gut morphology to counteract the effects of food quality.

The final chapter of this dissertation examined the distribution and abundance of *T.brichardi* within and among sites. Variation in fish abundance is expected to reflect the availability and quality of food. If algivore growth is limited by nutrient rather than energy acquisition, and if there is a substantial metabolic cost due to consumption of poor nutritional food, then habitats with high concentrations of N and P in the algae should support higher densities of algivores.

CHAPTER ONE

An experimental study of the relative influence of algal quality and quantity on the growth rate of juvenile fish (*Tropheus moorii*)

1.1 Abstract

The diet of primary consumers necessarily has a low concentration of nitrogen (N) and phosphorus (P) relative to carbon (C). Primary consumer growth can be limited by the intake of calories (carbon), N or P depending on the ratios of these elements in their diet. Algivorous fish in the littoral zone of Lake Tanganyika specialize on attached algae growing on rocks and the nutrient content of these algae vary across environmental gradients. We assessed the effects of food nutritional quality and total ration (quantity) on growth and excretion rate of *Tropheus moorii* fingerlings. The experiment was carried out in a photoperiod of 12:12 hours light: dark cycle in the laboratory for 7 weeks. Each fish was isolated in a single tank to control feeding, but all tanks were connected in a flow through system to standardize water chemistry and temperature (24 °C ± 2°C). We assessed the effect of diet ration and quality on daily growth rate using ANCOVA and regression analysis. Growth rates of *T.moorii* were positively correlated to phosphorus concentration in the diet ($F_{(1,40)} = 4.8$, $P < 0.05$). Food quantity became important at high food quality only. Thus, there was no advantage to the fish of simply consuming more food if the phosphorus concentration of the diet was very low. The proportion of daily P

intake lost through excretion was negatively related to the P content of the diet. The strong negative effects of poor food quality on *Tropheus* growth suggests the possibility for a long term negative effect of climate change that alter algal stoichiometry in Lake Tanganyika by reducing nutrients availability. This negative effect may strongly influence fish distribution and abundance through changes in growth rates. This may indirectly regulate carnival growth in a food chain because nutrient imitation at primary consumer's level can travel up the food chain (Chool, 2010), thus herbivore feeding on low quality food (high C:P) are in turn low quality food for other organisms in the food chain.

1.2 Introduction

The diets of herbivores are rich in carbon (C) relative to nitrogen (N) and phosphorus (P). Due to the relatively low nutrient concentrations of a plant-based diet, primary consumer growth can be limited by the intake of critical macronutrients, rather than energy (Sterner and Hessen, 1994). In addition, a plant-based diet also incurs substantial metabolic investments in digestion and foraging (Whelan and Brown, 2005). The rapid metabolic turnover of C relative to N and P in herbivores makes it difficult to determine *a priori* whether a given diet limits an herbivore's growth through low nutrient concentration (quality) or low energy availability (quantity or ration). Stoichiometric ratios have been used by ecologists to assess diet quality. However, although plants and algae are rich in C compound, many structural carbon compounds of plants and algae have low digestibility (Sterner and Elser, 2002). Thus, diet stoichiometry provides only a coarse first assessment of the dietary limits on growth.

There is continued debate about whether total energy intake (quantity) or diet nutrient content (quality) is more important for herbivore growth (Boersma and Kreutzer, 2002; Bukovinsky et al., 2012). For example, Vos et al., (2000) on midge species indicated that energy content (quantity) of the algal food is more important for herbivore growth when P is limiting. On the other hand, Kilham et al., (1997) and Boersma and Kreutzer (2002), reported that at low food quantity, both energy intake and nutrient content of the food is important. Sterner and Robinson, (1994) and Rothhaupt, (1995) did

not find any significant differences in growth rate when daphnia and rotifer were fed either high or low quality diet at low food quantities. The amount of energy (C) required for maintenance also varies with food quality. Maintenance costs for herbivores were higher when they were fed a diet with low P concentration (Boersma and Kreutzer, 2002). This metabolic cost probably reflected the high amount of energy required to process the P-limited diet.

Microalgae are more palatable and have a higher food quality than macro algae or terrestrial plants (Cebrian et al., 1999). Algae use light energy to fix carbon dioxide during photosynthesis and they assimilate inorganic nutrients such as N, P and silicon (Si) from the surrounding environments (Sterner et al., 1997; Cross et al., 2005). However, nutrient uptake by algae and carbon fixation during photosynthesis are not perfectly linked. Thus, although microalgae have high food quality relative to other types of primary producers, there is still a large variation in C: N: P ratio of algae (Frost et al., 2002). According to the Light-Nutrient Hypothesis (Sterner et al., 1997), at low light, P content of algae may increase because of an increase in phospholipid production resulting from photo-acclimation (Dickman et al., 2006). The resulting decrease in C to nutrients ratio leads to a high nutrient content for algae grown under low light conditions (Dickman et al., 2008; Fanta et al., 2010). In contrast, at high light intensities, high rates of photosynthesis lead to the accumulation of C-rich compounds, making periphyton a poor quality food (Hessen et al., 2002; Sterner and Elser, 2002). Thus, natural variation in

algal stoichiometry may generate variation in the growth rates, and degree of nutrient limitation, of primary consumers.

Algivorous cichlids in Lake Tanganyika are highly active, aggressive fish that spend the majority of their time actively foraging (swimming and grazing) on attached algae, or periphyton. Their gastrointestinal tract is long relative to predatory fish (Wagner et al., 2009) and usually contains food. The high costs of digestion, foraging activity and basal metabolism associated with life in this warm-water lake must be met by high energy intake. Thus, although the quality of Lake Tanganyika periphyton appears low relative to the protein-rich diet of a carnivore, both nutrient limitation and energy limitation of growth in herbivorous fish are plausible. Fish needs phosphorus for bones, teeth and scales development. P is also important for protein synthesis; however, herbivorous fish has higher P in their body tissue than their prey.

We conducted an experimental study to test the relative influence of algal quality and/or quantity on the growth rate of juvenile algivorous cichlid fish (*Tropheus moorii*), a species commonly found in Lake Tanganyika. We used a mixture of algae collected from Lake Tanganyika and laboratory grown cyanobacteria supplemented with vitamin and krill. We expected that the high costs of digesting poor food will require high energy intake; hence the growth rates of *T.moorii* may be determined by both nutrient and energy availability on the other hand, if energy is important, then the HB diet should have higher growth rates than the LG diet. If total phosphorus consumption is important, then fish raised in the LG and HB treatments should have similar growth rates. Finally, if the

concentration of P in the diet is important and there is a cost to consuming more carbon to meet the need for P, then fish in the LG treatment should have higher growth rates than in the HB. The maintenance costs of *T. moorii* will be negatively related to algal quality reflecting high digestion costs of a low quality diet. High C:P ratios in food increase the assimilation efficiencies of P and reduce their excretion rates from *T.moorii* (Elser and Urabe, 1999, Frost et al., 2004). Based on a stoichiometric perspective, we predict a decrease in P excretion rates from fish fed poor food quality.

1.3 Methods

I raised juvenile *Tropheus moori* for 7 weeks on composited algal diets that had one of four molar C: P ratios (148, 240, 346, or 513). Diets were fed directly to individual fish at a ratio of either 50% or 70% of the fish's dry weight (0.2 x wet weight).

Development of algal diets

I composited algal diets from bulk periphyton samples collected directly from rocks in Lake Tanganyika combined with mixed algal cultures grown in the lab. I collected rocks from a shallow depth (< 1.5 m) at Jakobsen's Beach (site 3 in Corman et al., 2010) in Lake Tanganyika and scrubbed the periphyton from the rocks using a nylon brush. The slurry was frozen for transport to the USA, and subsequently freeze dried.

I also cultured algae in the lab in 150 liter tanks at 12 : 12 hours light-dark cycles using CHU medium half strength #10 (Andersen, 2005). Tanks were inoculated with cyanobacteria from Lake Tanganyika and diatoms from UTEX (University of Texas at

Austin). I cultivated algae at 3 phosphorus concentrations (1, 10, 100 µL P /L) in order to produce algal diets with different C: P ratios. Algae were harvested twice per month. To harvest, I scrubbed algae from the walls of the tank using a brush with a long handle, then, waited for 30 min to allow algae to settle at the bottom of the tank. I harvested algae by opening an outlet at the base of the tank. After every harvest, I refilled the tank with clean Chu medium and phosphorus based on the amount of water replaced in the tank. Algae were freeze-dried at -30^{o}C (Virtis, Gardiner, NY) and analyzed for C: N content using an elemental analyzer (Elemental Americas, corporation, NJ, USA). Periphyton P content was analyzed using the acid molybdate method for particulate samples (APHA, 1995). Duplicate subsamples (~ 5 mg) were combusted for 1 hour at 500 °C and then digested in acid for 2 hours at 102 °C. Absorbance was read at 880 nm on a micro plate reader (Bio-Tek Instruments, Winooski, Vt). C:N:P ratios of algae from each harvesting event were analyzed separately. Batches of algae with different C:P ratios were then quantitatively mixed to produce diets with target C:P ratios. I attempted to keep N: P ratios in the diets similar to N:P ratios in Lake Tanganyika periphyton (N:P = 29). I added a small amount of freeze dried krill (San Francisco Brand) and commercial fish vitamins to each diet (Table 1.1) to reduce the chances of trace element or essential amino acid limitation.

Growth experiments

We formulated 4 algal diets by mixing different amounts of Lake Tanganyika algae, cultured algae, freeze-dried krill, and vitamins (Table 1.1). Each diet had a

different C:P ratio: 513 (Very Bad, VB); 346 (Bad, B); 240 (Good, G); and 148 (Very Good, VG). We attempted to keep N:P ratios constant between 29-34, but the VG diet had a slightly lower N:P ratio (14) because it had a lot of krill in the mixture which contributed to high protein levels. A preliminary 6-week feeding experiment revealed that *Tropheus* required at least 40% of their body dry weight (DW) per day in order to grow on the algal diets. Based on this experiment, we assigned each fish either a low ration (L = 50% DW/d) or a high ration (H= 70% DW/day). The diets and rations were formulated such that the High ration Bad diet and the Low ration Good diet had the same amount of N and P; however, HB food had 40% higher C content (C: P = 346 and 240 respectively) (Table 1.2). Food was prepared in the form of flakes and fed to the fish in dry form. Sixty juvenile *T. moori* (mean weight = 0.2 g wet mass) were obtained from a fish dealer and held in a common tank for 21 days. Immediately before the start of the experiment fish were ranked from smallest to largest. Then, each fish within groups of six similarly sized fish was randomly assigned to a daily ration and diet of 2 * 2 factorial (LB, HB, LG, HG) plus two complimentary extreme diets (HVB and LVG) to extend the range of quality-quantity variation (Table 1.2). Throughout the experiment, each fish was kept in an individual 10 gallon glass tank connected in a flow through system, kept under 12:12-hour light-dark cycle, thermostatically controlled at 24 ± 2 °C. Each treatment contained 7 to 9 replicates. Fish were fed in small dishes two times per day. I weighed each fish once each week and adjusted the amount of food to reflect the new weight. At the end of the experiment, I assessed an individual fish growth rate (per day) by measuring the rate

of change of animal body mass starting from week 3 to week 7 using the following equation:

$$Daily\ Growth\ Rate = exp\ (log\ (w2/w1)\ /\ (t_2\text{-}t_1))$$

Where w2 and w1 are the final and initial weights (week 7 and week 3 respectively, because fish require an acclimation period after the initial diet switch); t_2 and t_1 are initial and final time (days) respectively.

Table 1.1: Algal food formulation with different C:P ratios to reflect values in Lake Tanganyika. Bad and Good food contain 17% Lake Tanganyika algae, whereas Very bad and Very good contained 80% and 9% Lake Tanganyika algae respectively

Treatments	Very Bad (VB)	Bad (B)	Good (G)	Very good (VG)
Krill	2%	2%	2%	31%
Lake Tanganyika	80%	17%	17%	9%
Lab. Culture algae	17%	80%	80%	59%
Vitamin	1%	1%	1%	1%

Table 1.2: Daily food ration (mg/g) for very goof (VB), bad (B), good (G) and very good (VG). The HB and LG had the same %P, and % N, however, HB had 1.4 times higher % C than LG. The LVG and LG had similar % C and % P, however, the former had 1.9 times higher % P. Good and Bad are 2 levels of quality * 2 levels of quantity - block design.

			Quality			
			VB	B	G	VG
		mg/g/day	C:N:P = 513:34:1	C:N:P =346:29:1	C:N:P =240:29:1	C:N:P =148:14:1
Quantity	50% BW	C		254.6	258.7	283.6
		N		23.5	33.7	34.3
		P		1.76	2.5	5.1
	70% BW	C	244.9	380	386	
		N	19.1	35.1	50.3	
		P	1.2	2.6	3.7	

Excretion rates

I measured ammonium and phosphate excretion rates of each fish on the final day of the experiment. An individual fish was put into a 500 mL zip lock bag filled with 300 mL pre- filtered aquarium water (0.7 μm) and incubated for 30 minutes. Then, two samples (40 mL) of incubated water were collected from each bag by filtering through a GF/F syringe filter. I froze one sample for P analysis, and I immediately assessed the other sample for NH_4 concentration. At the same time, three bags, each containing 300 mL of filtered tank water without fish, was incubated as a control. I assessed Ammonium fluorometrically according to Holmes et al., (1999). Phosphorus was quantified using the

molybdate-blue method after high-temperature persulfate digestion (APHA, 1995). Excretion of N and P were defined as the difference between initial and final nutrient concentrations. Excretion values expressed as P and N (µg/hr/g fish) for each treatment were then related to the log transformed weight of the fish and food quality and quantity. N: P molar ratio of excretion rates was also determined. The percentage daily dietary P excretion was calculated from the relationship between estimated daily P excreted (24 x measured hourly rate) divided by daily P ration in the food provided each day.

Data analysis

I assessed the influence of food quality and quantity (ration) on changes in fish weight (g) over time using a linear mixed effects model (Bates et al., 2012). I entered food quality, quantity and time (with interaction terms) into the model as fixed effects and fish number as a random effect. Visual inspection of residual plots did not reveal deviations from normality. P-values were obtained by likelihood ratio tests of the full model with the effects in question against the reduced model without the quality and quantity effects in the model. I quantified the effect of diet quality and quantity on relative growth rates (RGR). For this analysis, I restricted the treatments to LB, HB, LG and HG only and used a two-way ANOVA (2 * 2 block design Table 1.2). Subsequently, the effect of algal food P content on growth rates was analyzed using a one way ANOVA.

I used ANCOVA to tests for the significant effects of food treatments and fish weight on N (ammonium) and P excretion rates, N: P molar ratio. P, N: P molar ratio and

fish weight was log transformed to increase homoscedasticity of residuals. We used Tukey multiple comparison tests to determine which treatment differed when significance was observed. All data analyses were done in R (R Core Team 2013).

1.4 Results

Fish growth

At the beginning of the experiment all treatments had similar initial mean weights (grams). For the first few weeks, fish acclimated to the diet shift, and some fish did not eat all of the food provided, hence fish decreased in weight. After 7 weeks, fish weight was significantly different among treatments (Fig 1.1). In all treatments fish weight increased with time (mixed model ANOVA, Table 1.3). However, the increase in weight differed between treatments. This was indicated by the mixed model interaction (Quality*Time and Quantity*Time; Table 1.3). The interaction between quality * quantity *time was not significant.

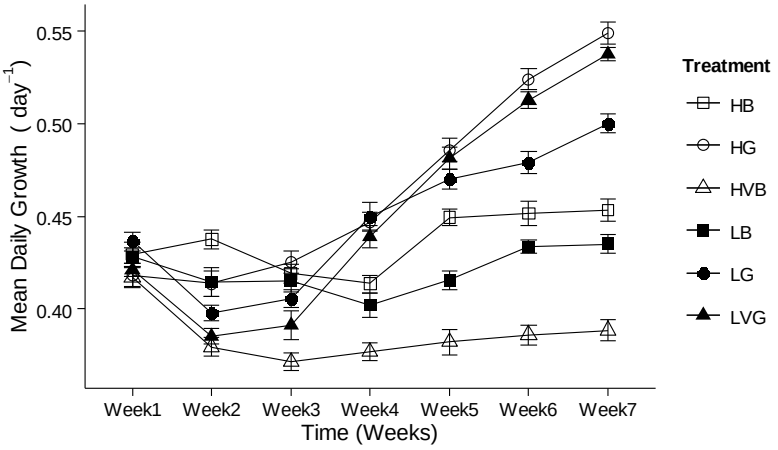

Figure 1.1: Mean fish weight (g) for low bad (LB; n = 10), low good (LG; n = 7), low very good (LVG; n = 7), high bad (HB; n = 7), high good (HG; n = 7) and high very bad (HVB; n = 7). Experiment conducted for 7 weeks. Error bars represent standard error of the mean.

Table 1.3: Analysis of variance (ANOVA) of the relationship between periphyton quality, quantity (2 levels of quality * 2 levels of quantity) and time (weeks) on fish weight. Significant effects are marked in boldface type.

Parameter (Log weight)	SS	MS	F value	P value
Quality	0.0011	0.0011	0.2693	0.6068
Quantity	0.0002	0.0002	0.0476	0.8284
Time (Week)	0.0778	0.0778	19.2865	**0.0035**
Quality*Quantity	0.0003	0.0003	0.0801	0.7786
Quality*Time (Week)	0.0294	0.0294	7.2841	**0.0076**
Quantity*Time (Week)	0.0119	0.0119	2.9371	**0.0883**
Quality*Quantity*Time (Week)	0.0106	0.0106	2.6206	0.1072

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

Fish fed good diets (G and VG) had significantly larger size after 7 weeks than fish fed bad (B) diet in both high (70%) and low (50%) treatments i.e. there was a significant quality effect ($p < 0.05$, Fig 1.1). The two-way factorial ANOVA between good and bad food revealed that the slope of the mean weight of *T. moorii* in good (G) quality food was significantly higher by 0.03 ($p < 0.05$) at the end of experiment than in bad (B) quality food, and was higher by 0.02 ($p < 0.05$) when fed high (70%) quantity than when fed low (50%) quantity of food.

The relationship between daily growth rate (DGR) and food revealed that both quality, quantity and the interaction between food quality and quantity were significant (quality * quantity; $F_{1,25} = 4.1$, $P = 0.04$, Table 1.4), suggesting that fish growth rate deferred when fed different food quality based on food quantity. Fish given good food at high quantity (HG) grew better and experienced increase in growth (mean DGR = 1.0075 ± 0.0008) than when fed good food at low quantity (LG) (mean DGR = 1. 0043 ± 0.0004). The difference in growth rates was not significant between high bad (HB) and low bad (LB) ($p > 0.05$; Fig.1.2 & 1.3, DGR = 1.00235 and 1.0024, respectively).

Table 1 4: ANOVA results for the effect of food quality and quantity on daily growth rates of *Tropheus moorii* from week 3 to week 7. Using 2 levels of quality * 2 levels of food quantity (LB, HB, LG and HG). Significant effects are marked in boldface type.

Response : DGR					
	DF	SS	MS	F value	P value
Quantity	1	0.000021	0.000021	5.119900	**0.0325**
Quality	1	0.000086	0.000086	20.617200	**0.0001**
Quantity*Quality	1	0.000019	0.000019	4.540800	**0.0431**
Error	25	0.000104	0.000004		

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

Daily growth rates (DGR) were positive and strongly related to the P concentration of the food (Fig. 1.3, 1.4 and 1.5). Feeding higher quality diets with high P concentration resulted in higher daily growth rate DGR ($F_{1,25} = 23$, $p < 0.05$). DGR increases with a decrease in C:P, with an increase in mg P/g fish/day and with increase in P content (%), suggesting that phosphorus growth efficiency increases with decrease in C:P molar ratio of the food. Fish grew significantly more when fed good quality with low C:P (mean DGR for G = 1.0058) than when fed bad quality food with high C:P (mean DGR for B =1.0023) at either ration size. A small amount of high quality food (LG) met nutritional requirements for growth, (DGR = 1.0043) but the highest growth rates were observed when given HG (DGR =1.0074). Mean DGR was 40% lower in fish fed a low ration of bad food (LB) compared to a low ration of good food (LG), despite the two

foods having the same carbon content (Fig.1.2). The growth rate of fish in the LG treatment was higher than that of HB despite the two treatments having the same daily P but HB has higher P concentration per unit carbon.

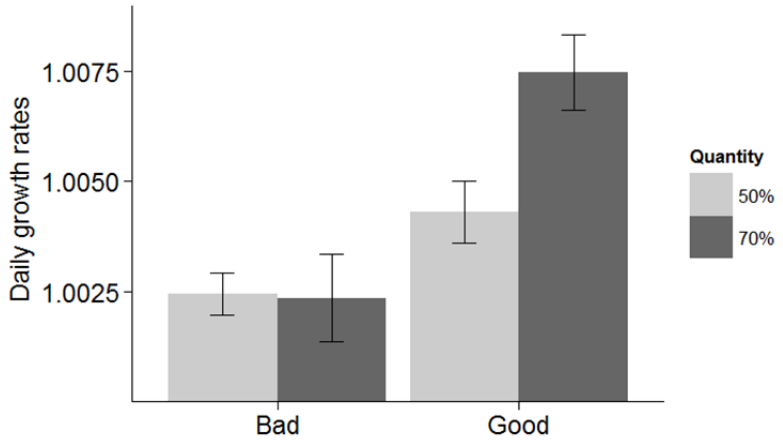

Figure 1.2: Mean daily growth rate (DGR) of *T. moorii* fed Bad or Good food at either low (50%) or high (70%). Error bars represent standard error of the mean. DGR was calculated between 21 days after the start of the experiment (week 3) and 49 days (week 7)

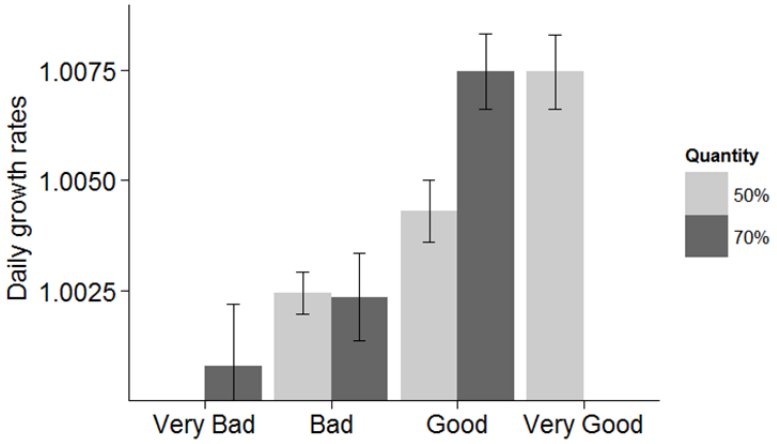

Figure 1.3: Mean daily growth rate (DGR) of *T. moorii* fed different food treatments. Error bars represent standard error of the mean. DGR was calculated from week 3 to week 7.

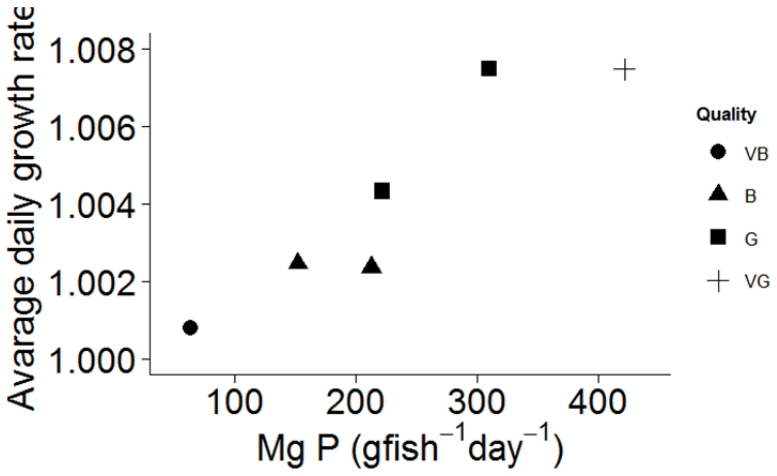

Figure 1.4: Relationship between Mean daily growth rate of *T. moorii* and total P content of the food (calculated as % P * food ration (50% or 70%) *1000) of each treatment over 35 days.

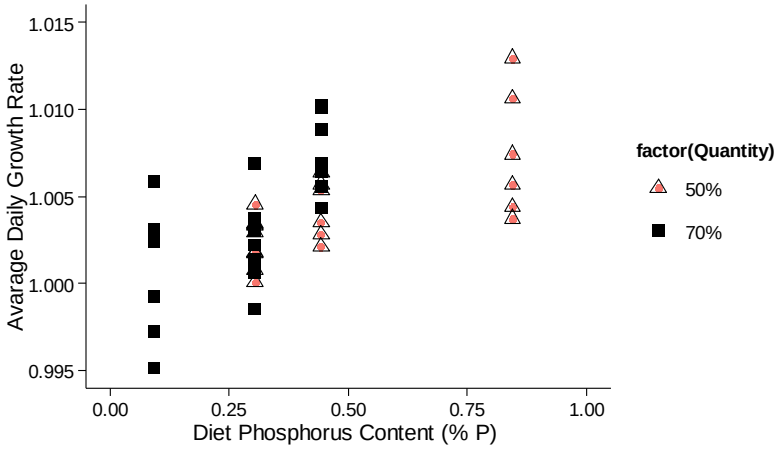

Figure 1.5: Relationship between mean daily growth rate (DGR) of *T. moorii* and phosphorus content (%) for high (70%) and low (50%) food quantity.

Fish fed the LVG diet had a higher growth rate (DGR = 1.0074 ± 0.0008; Fig.1.3) than LG (DGR = 1.004 ± 0.0007). We found no differences in growth rates between individual fish when fed bad food (B) or very bad (VB) food qualities in any quantities (LB, HB or LVB). Fish fed LVB food had the lowest DGR (1.0007 ± 0.001), and phosphorus-limited food (B) had a negative effect on *Tropheus* growth regardless of quantity (Fig. 1.2 & 1.3).

Fish excretion rates

Phosphorus mean excretion fell between 0.2 and 0.6 µg P/hr/g fish, Ammonium was 1 and 2 µg N/hr/g fish and the excreted N: P ratios was between 4 and 21. The N:P ratio of excretory products was much lower (20, 6 and 21 for VB, B and G food

respectively) than the values ingested from the food (32, 29, 29 for VB, B and G food respectively). Fish fed VG had N:P excretion values that were the same to N:P of their food (N:P = 14).

Although it was not statistically significant, we found that fish excretion rates of N (ammonium) and N:P decrease with increase in N:P of the food ($r = -0.2$, $P = 0.7$), whereas P excretion increases with N:P of the food ($r = 0.15$, $p = 0.4$). Our results also shows that N (Ammonium) and N:P excretion increases with increase in log-fish body size ($p < 0.05$, Fig. 1.7 & 1.8; Table 1:5). However, log-body size did not affect phosphorus excretion ($p > 0.05$; Fig. 1.6, Table 1:5).

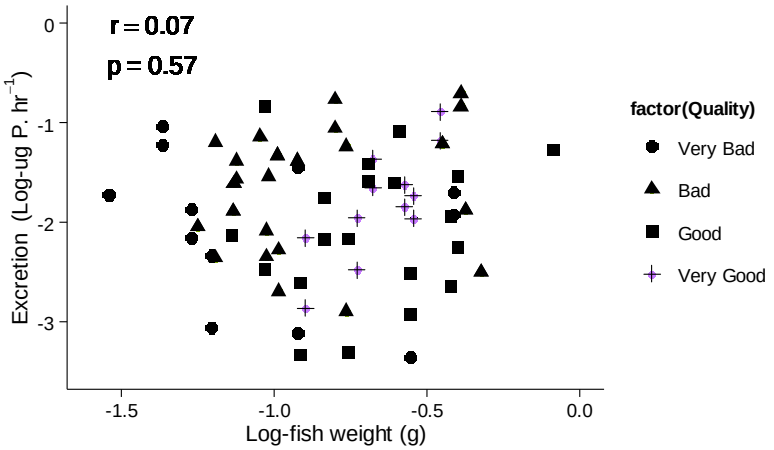

Figure 1.6: P excretion rate (µg P / hr) and log-fish weight for the very bad (VB), bad (B), good (G) and very good (VG) food.

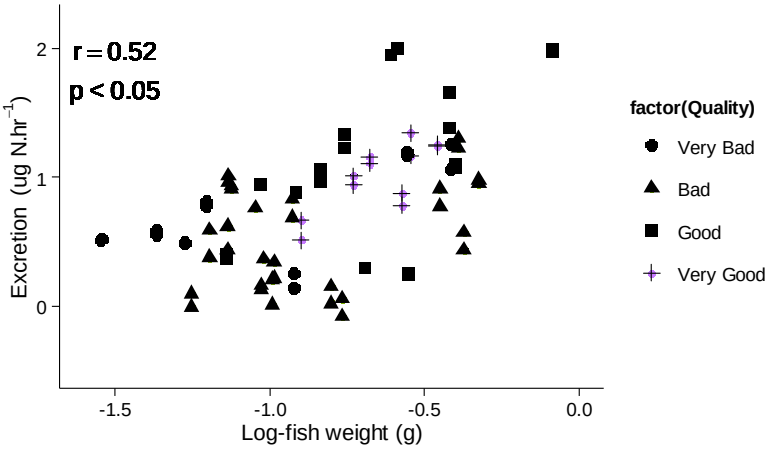

Figure 1.7: N excretion (µg/hr) and log-fish weight for the very bad (VB), bad (B), good (G) and very good (VG) food.

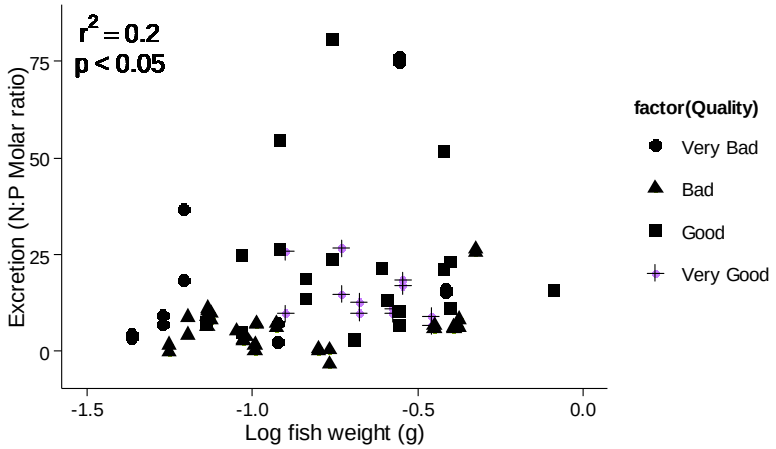

Figure 1.8: N: P excretion and log fish weight for very bad (VB), bad (B), good (G) and very good (VG) food. The relationship is significant, mainly driven by VB and G food.

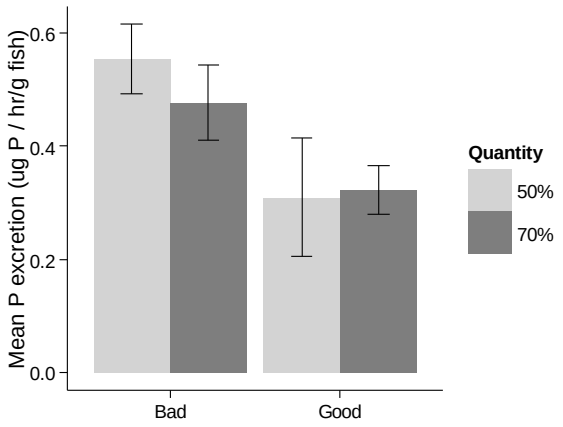

Figure 1.9: Mean mass P specific excretion (ug P $hr^{-1}g\ fish^{-1}$) of *T. moorii* at diferent food quality (G and B) and quantity (50% and 70%). Error bars represent standard error of the mean.

There was a significant effect of food quality and quantity on ammonium excretion rates (µg N/hr/g fish). Marginally lower rates of ammonium were excreted when fish fed on low quantity of food than high quantity ($F_{(1,50)} = 3$, P = 0.08, Fig. 1.10)**.** However, quantity did not affect P excretion rate and N:P excretion ratio, and there was no significant interaction effect (quality * quantity, $p > 0.05$). Mass-specific P excretion rate (µg P/hr/g fish) was negatively related to food quality ($F_{(1,50)} = 4.5$, $p = 0.03$, Fig.1.9). Higher P excretion rates were observed when fish were fed bad food quality ($p < 0.05$). The N:P ratios of excretory products was significantly higher when fed good food quality than bad ($F_{(1, 50)} = 15.8$, $p = 0.002$, Fig. 1.11).

When considered as % of food consumed, the proportion of daily dietary P excreted decreased with food quality. Feeding high quality food (G), fish retained more

phosphorus in their body, whereas with bad food (B), fish excreted a greater proportion of the daily P ration (Fig. 1.9,1.12 & 1.3).

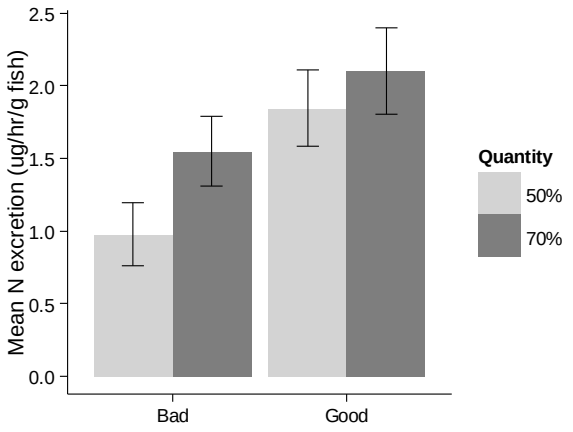

Figure 1.10: Mean mass N specific excretion (ug N hr^{-1}g $fish^{-1}$) of *T. moorii* with food quality (G and B) and (B) quantity (H and L). Error bars represent standard error.

Table 1.5: Results of ANOVA to predict the relationship between P and N excretion rates and N: P ratio excreted when fish were fed LB, LG, HB and HG (2 quality*2 quantity-block design).

Phosphorus (ug/hr)	Df	SS	MS	F value	P value
Treatments	5	0.086	0.017	1.701	0.146
Log-weight	1	0.012	0.012	1.227	0.271
Treatment*Log-weight	5	0.152	0.030	2.995	0.016 *
Error	68	0.690	0.010		
Nitrogen (ug/hr)					
Treatments	5	5.647	1.129	9.153	< 0.5 ***
Log-weight	1	3.138	3.138	25.436	< 0.5 ***
Treatment*Log-weight	5	1.920	0.384	3.112	0.013 *
Error	68	8.390	0.123		
N:P molar ratio					
Treatments	5	3653.200	730.640	3.482	0.007 **
Log-weight	1	1031.700	1031.670	4.916	0.029 *
Treatment*Log-weight	5	1871.000	374.200	1.783	0.127
Error	68	14269.200	209.840		

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

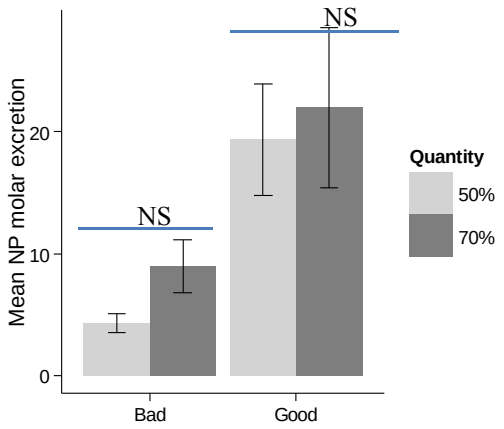

Figure 1.11: Mean N: P molar excretion ratio for *T.morrii* consuming the Bad and Good food at low (50%) and high (70%) quantity. Error bars represent standard error of the mean. NS letter represent not significant between low and high quantity. Significantly deference was observed between bad (B) and good (G) food.

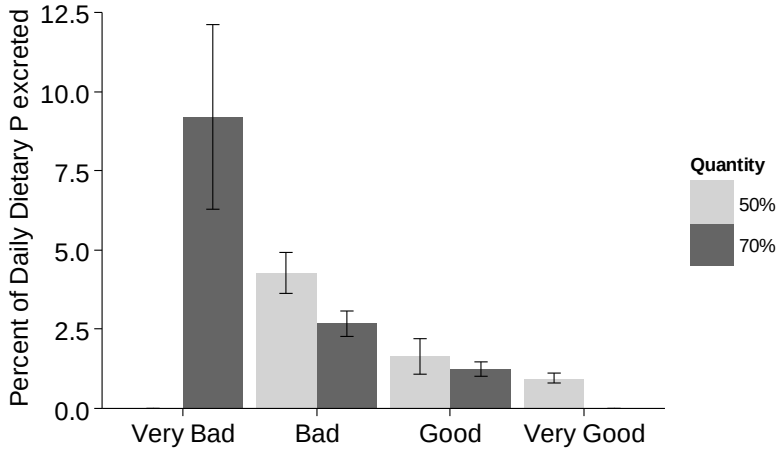

Figure 1.12: Percent of dietary daily P excreted for Very bad, Bad, Good and Very good food. Error bars represent standard error of the mean.

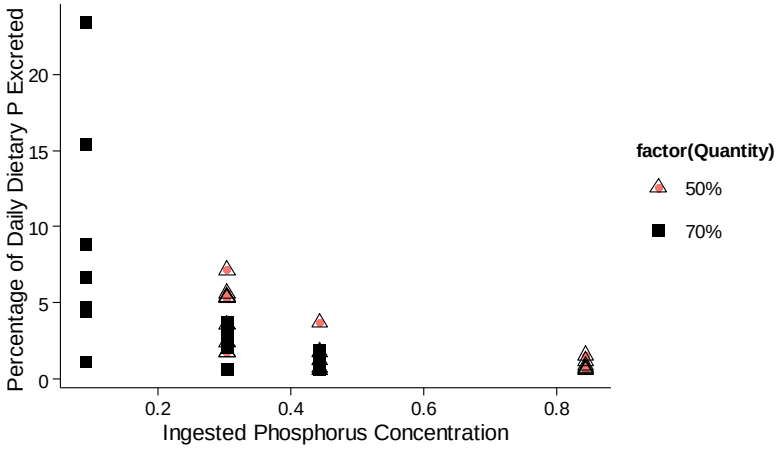

Figure 1.13: Percentages dietary daily P excreted in relation to P concentration of the food.

1.5 Discussion

The diets were formulated to test some very specific hypotheses. The high quantity bad food (HB) and low quantity good food (LG) had the same amount of N and P but the HB had 1.4 times higher C content. Overall fish growth rates were most strongly correlated with %P in the diet. Quantity was only important when given good food quality.

Good quality food (G) met a nutritional requirement for growth at either quantity. However, high quantity (HG) resulted in higher growth that the lower ration LG (Fig.1.2). On the other hand, a high quantity (H) of very bad food (VB) did not increase the growth rate of *T. moorii*. This substantiates previous finding that the growth rate of primary consumers is strongly influenced by quantity only when food has a sufficient nutrient content (Sterner, 1997). Lower food quality reduced relative growth rates. When fish are fed poor or bad food, there was no compensation by simply increasing the amount of food as proposed by Brett (1993). Giving high quality (G) at high quantity (H) significantly increased fish growth rate suggesting that quantity begins to matter at a threshold of diet quality. In my study, this occurred when fish consumed a diet of > 0.5% P, which is well below the optimal diet P content of 1.5% for herbivorous fish (Benstead et al., 2014).

The finding that dietary phosphorus impacted *Tropheus* weight gain (Fig. 1.1) is consistent with other studies in insects and zooplankton (Frost and Elser, 2002; Demott et al., 1998; Elser et al., 2001), where feeding on phosphorus enriched food exhibited elevated growth. Good food increases fish growth at low and high quantities. However,

high quantity of good (HG) had higher growth rates than LG. Our results are in agreement to Boersma and Kreutzer, (2002) and Achary et al., (2004) who found that food quality influences *Daphnia* growth rate even at very low food quantities. High food quantity contains a high concentration of phosphorus, which may contribute to high growth rates.

The positive relationship between specific growth rates and food P-content in food is in agreement with the prediction of the growth rate hypothesis (GRH) that faster growing organisms require more P (Sterner and Elser, 2002). The Ribosomal RNA in invertebrates often constitutes a major fraction of body P. Since ribosomes are the sites of protein synthesis, high P content in good food could allow more protein synthesis and thus, a high growth rate. This may result in a positive correlation between the P-content of the food, body tissue and the growth rate of *Tropheus* (Elser et al., 1996, 2000; Sterner et al., 1995).

When given high quantity of bad quality food (HB), *T. moorii* did not grow any faster than when given a low ration of bad food (LB). In fact, the growth rate was slightly lower. This result is contrary to zooplankton experiments, where zooplankton compensated for bad quality diet by eating more food thus increased their growth (Boersma and Elser, 2006; Brett, 1993; Fink and Von Elert, 2006). Low growth rate may be due to the increase in physical and morphological digestion costs of bad food (López-Calleja, et al., 2000). High digestion costs of the poor P food may increase the metabolic costs on the animal. In addition, the significantly increase in excretion rates of P when

fed bad food (Fig. 1.7) may exhibit a decrease in growth of a consumer as proposed by Karasov (1996), especially when there is a stoichiometric imbalance in a diet due to the presence of high dietary nutrients. The assimilation efficiency depends on the digestibility of the food; the presence of cellulose, chitin, lignin or other undigestible material (e.g sediment) in the poor quality food may reduce assimilation efficiency while increases the digestion costs (Bayen et al., 1986). Bad food probably increased the amount of energy required to process the P-limiting diet.

Consumer's nutrient excretion is influenced primarily by an organism's nutrient composition as well as an organism food. Feeding algivores a very high P diet can lead to a decrease in phosphorus absorption or an increase in phosphorus excretion (Sterner et al., 1992; Sterner and Elser, 2002). Herbivorous fish actually grow more slowly when fed diets with > 2 % P (Benstead et al., 2014). My results demonstrate that this increase in P excretion also occurs when fish are fed very poor quality diets, suggesting poor nutrient use efficiency.

There was a positive relationship between nutrients excretion rates and food quality suggest that excretion rates depend on weight of an individual fish. When fish were fed good quality food, fish retained more dietary P than when fed poor quality food. Phosphorus excretion is expected to be high in poor quality food if a larger fraction of the ingested phosphorus is never absorbed as food passed through the gut (Messmer et al., 2011) due to either poor food digestibility or poor extraction efficiency. Poor growth rate when fed very bad food (VB) may be also due to the presence of sand in the food. It was

not possible to scrub algae from the rocks without sand. Algae from Lake Tanganyika had 30% sands; this may have contributed to poor daily growth rates. Digestion of the poor food costs energy. The increase in energy expenditure may results from the increase in physical processing of food, increase in digestion, absorption and synthesis of excretion products all these activities incurs energy.

I found no significant relationship between food nutrient element and excretion N:P ratio, suggesting that other factors than food, such as differenced in body requirements and food assimilation efficient may alter excretion rates of nutrients. Another potential factor that may cause dietary effects on excretion is fish size differences (Torres and Vanni, 2007; Villeger et al., 2012). Excretion rates (μg N/hr) increased with increase in log-fish weight. The differences was caused by differences in organismal growth and feeding varied based on weight which may cause differences in excretion ratios in natural settings.

This study reveals that the growth rate of primary consumers is strongly influenced by quantity only when food has a sufficient nutrient content. Lower food quality reduced the daily growth rate of the fish. High amount of poor quality food did not compensate for poor quality effect. Our study also suggests that dietary elemental composition can play a significant role in altering nutrient excretion rates and ratios. Poor food quality caused P assimilation efficient to decrease hence decrease in growth rate.

This study provided a highlight on the effect of food on growth and excretion rates using a wide range of food, more careful study of the effect of food quality in the

field across a range of diets are needed because anthropogenic activities due to climate change may impact the food resources and changes their quality. The decrease in food quality may negatively affect consumer-driven nutrient recycling, and fish growth rates which is important to ecosystem function.

CHAPTER TWO

Behavioral and morphological gut structure of fish (*Tropheus Brichardi*) in relation to food quality across sites in Lake Tanganyika.

2.1 Abstract

Anthropogenic changes in primary producer quality due to reductions in nutrient loading and increases in terrigenous sediments may alter the nutritional value of attached algae at the base of the food chain in the littoral zone of Lake Tanganyika. Animals may compensate for low food quality by becoming more selective, increasing ingestion rate, or through compensatory changes in gut morphology. Optimal foraging theory predicts that animals will modify their behavior to maximize energy and nutrients intake per unit time. We assessed the influence of periphyton quantity and nutritional quality on the amount of time devoted to feeding, the duration of feeding bouts and the feeding rate (bites/sec) during an individual feeding event of *T.brichardi* in Lake Tanganyika using a linear regression model. We assessed the relationship between food quality and relative intestine length, stomach fullness and condition factor. Our results reveal that algivores respond to variation in food quality through both behavioral and morphological modifications. Algivores fed selectively on diatoms, which are rich in essential fatty acids (EFA) at all sites, but fish at sites with poor food quality (low %P) spent less time feeding in each bout. There was a positive correlation between sediment accumulation on the

periphyton and both gut length and stomach fullness. The increase in relative intestinal length may facilitate a more complete extraction of nutrients and energy. High fish density in high quality sites tends to increase the feeding pressure, this may affect algal biomass. However, the combined effects of lower algivore densities and lower feeding rates along a gradient of sediment accumulation led to a decrease in grazing pressure at high sediment sites. Sediment covers and dilutes algae, thus deplete the algal quality. This may increase the digestion costs to herbivores; consequently, produce negative cascading effect through the food chain.

2.2 Introduction

Climate change is reducing the frequency of upwelling events in Lake Tanganyika, and these incursions of nutrient-rich deep water are a critical source of nitrogen and phosphorus for algae (O'Reilly et al., 2003, Verburg et al., 2003). Reduction in internal loading of nutrients may directly reduce periphyton nutrient content (quality) and/or productivity (quantity) in the littoral zone. In addition to the reduced nutrient loading, much of Lake Tanganyika's littoral habitat is experiencing increased sediments load due to deforestation of the watershed (Alin et al., 1999). The removal of vegetative cover results in increased erosion of the soil sediments which are deposited in water bodies. For example, sediment accumulation at rocky littoral sites adjacent to fishing villages outside of Mahale Mountains National Park (MMNP) was 5 times higher than at nearby sites within the park with intact riparian vegetation (McIntyre et al, unpublished). Fish diversity and species richness was much higher in the protected sites within MMNP compared with village sites (Sweke, 2013). Although the difference in fish densities reflects, in part, differences in fishing pressure, it is notable that algivorous fish is the only feeding group that is showing long term declines in the Lake Tanganyika littoral fish community (Takeuchi et al., 2010). Algivores may compensate for reductions in algal quality by feeding more selectively and targeting high quality food patches. However, the efficacy of behavioral modifications may be limited if food availability or quality within a habitat is uniformly reduced. Furthermore, algivores probably have a limited capacity to

avoid ingestion of sediment during feeding (Lombardozzi, 2003) and this limitation is likely to interfere with their digestion and feeding behavior.

The way an organism allocates time to various activities affects its fitness because time allocated for one activity is unavailable for another (Herbers, 1981). The amount of energy and nutrients acquired per unit time are determined by both the time allocated for foraging activities (Abrams, 1984), and the quality and quantity of food. If foraging time is dedicated to non-foraging activities, growth rate will decline (Stevephens and Krebs, 1986). Food resources in the environment are unevenly distributed (DeVries, 1994) and occur in patches. Hence, the organism's foraging decisions take into account where to feed, the cost of travel time between patches, and the type and availability of food consumed (selectivity), and specifically how long to feed in a patch (Charnov, 1976). Optimizing foraging decisions allows animals to maximize energy intake per time to meet their nutritional body requirements (Karasov and Del Rio, 2007; Snellen et al., 2007). However, herbivores often consume carbon-rich, but nutrient-poor food, and optimal foraging theory can be used to assess whether herbivore foraging strategies are optimizing nutrient or energy intake (Plath and Boersma, 2001; Schatz and McCauly, 2007).

Herbivores consume food containing low phosphorus and nitrogen but high carbon relative to their body tissue (Hessen et al., 2002; Sterner and Elser, 2002). Algae vary their tissue nutrient composition based on light availability (Sterner et al., 1997), nutrient availability, and reproductive status (Acharya et al., 2004). Algae contain

structural carbohydrates (hemicellulose and cellulose) in their cell walls that are difficult for algivorous fish to digest (Sterner and Elser, 2002). There are substantial differences in both cell wall composition and storage materials among different taxonomic groups of algae. The taxonomic diversity of algae combined with plasticity in cellular nutrient within algal taxa leads to high variation in C:N:P and fatty acid content of algal communities that has profound consequences for algivorous animals (Sterner and Elser, 2002). High C:N:P or low essential fatty acid content of algae reduces growth rates and reproduction of algivores (Sterner, 1993; Urabe and Sterner, 1997). There is growing evidence that consumers will feed selectively on high quality algae in mixed algal assemblages (Schatz and McCauly, 2007).

Optimal foraging theory assumes that high quality diet is always available in the environment but is hard to find. A consumer makes foraging decisions based on food abundance, food distribution, predation risk, and social interactions (Whelan and Brown, 2005). Analysis of foraging decisions considers factors that occur prior to food consumption. In contrast, physiological approaches focus on factors that influence absorption of food after it has been consumed (Karasov, 1996, 1990), and argue that animals should optimize food absorption rather than food intake (van Gils et al., 2008) . There is within-species plasticity in gut morphology such that animals can change gut length in response to food quality (Wagner et al., 2009, van Gils et al., 2008), and animals can also alter the production of digestive enzymes in response to variation in food quality (Karasov and Del Rio, 2007). Finally, consumption rate itself may be a

strategy to optimize digestive efficiency rather than to maximize total intake (van Gils et al., 2008). Optimizing these post-consumption parameters related to digestion efficiency are not captured by optimal foraging theory.

The objective of this study is to assess algal nutritional quality and quantity at 12 sites and how foragers make feeding decision in a gradient of food qualities, food abundance and sediment accumulation. *T. brichardi* feeds on periphyton that is attached to the surface of rocks in the shallow wave zone. The surfaces of the rocks are covered in alga, but the density and taxonomic composition of the algae will vary based on water depth (light), the orientation of the rock surface, and the time since an area was last grazed (Power, 1984). When *Tropheus brichardi* encounters a rock surface it has to make a decision whether to stay and feed or continue swimming. Once the fish begins to feed in a patch, it can choose either to eat everything available or to move on when algal densities become low. During a feeding bout, the energy gain per time starts to decrease because food diminishes with time in a patch. The marginal value theory (MVT) predicts that animal should stay feeding in a patch as long as there is a maximum energy gain or maximum food intake per unit time (Charnov, 1976**;** McNair, 1982), but this can be extended to optimizing nutrient (N, P) acquisition per unit time (Schatz and McCauley, 2007). I hypothesized that if *T. brichardii* are maximizing energy intake, then the time spent per feeding bout should be correlated with periphyton standing crop. Conversely, if *T. brichardii* is maximizing nutrient acquisition rates, time spent per feeding bout should be unrelated to food abundance and positively correlated with food quality.

The rate of feeding of *Tropheus brichardi* during any feeding bout depends on whether the fish is selectively feeding on particular components of the periphyton or simply maximizing intake rate. The periphyton community in Lake Tanganyika is dominated by nitrogen fixing cyanobacteria and epilithic diatoms (Cocquyt and Vyverman, 2005; Hecky and Kling, 1986). *Tropheus* are thought to browse on the strands of the cyanobacteria and ingest some diatoms while doing so (Hori, 1983). However, diatoms, but not cyanobacteria, are rich in essential fatty acids (Brett and Mullar Navara, 1997). If *T. brichardi* are selectively feeding to maximize food quality then we expect that relative abundance of diatoms in the diet will be higher than in the environment. Furthermore, if *T. brichardi* becomes more selective as periphyton quality decreases, then feeding rate (bites per second) will be directly correlated with food quality. In contrast, there is no a priori reason to expect feeding rate to be correlated with food quantity. Rather, as noted above, if food quantity, or maximizing energy intake is important, then individual feeding bouts should be longer in environments with higher densities of food.

Algal food quality is generally assessed based on the carbon to nutrient ratio of the organic matter itself (Sterner and Elser, 2002). However, sediment accumulation on rocks indirectly reduces the nutritional value of periphyton by diluting the food resource with indigestible inorganic matter. We expect that increased sedimentation in a habitat creates a more heterogeneous food environment. If so, then fish in habitats with high sediment accumulation should spend more time searching for high quality patches. Any attempts to avoid ingestion of sediments would slow feeding rate (reduced bites/sec). However, it is

unlikely that the algivores can altogether avoid ingesting inorganic sediments. An increase in gut size facilitates a more efficient utilization of food because larger guts have higher surface area and allow longer food transit times, which enhance nutrients absorption (Sibly, 1981). *Tropheus brichardi* gut length as a proportion of body mass is closely correlated with the quality (C:N) of its organic food (Wagner et al., 2009). We hypothesized that the intestine length, standardized for fish size, would be positively correlated with inorganic sediment content of the periphyton.

2.3 Methods

Study sites

I assessed the activity budget of *T.brichardi* in the field and quantified algal food resource in the rocky littoral zone of Lake Tanganyika during the dry seasons (June – August) from 2012-2013 (Appendix A; Table 3.1). I monitored algivores' food at 12 spatially isolated rocky sites (> 1 km shoreline between sites) along 15 km of shoreline in the Kigoma region of Tanzania. I selected sites across a gradient of land use and wave exposure, two variables that are likely to affect nutrient and sediment retention in the shallow littoral habitat. Three southern sites (sites 2, 3, and 4) around Jakobsens beach resort and the southernmost site (13) at Kitwe point are bordered by Miombo forest mixed with grass, but experience a gradient of wave action depending on shoreline orientation to the prevailing winds. Site 6, near the village of Katabe, is protected from wind and wave action and surrounded by sparse grassland. Site 7 was located in a

protected bay with a very low slope and was obviously degraded by sediment from a hotel located at the top of an overhanging cliff (McIntyre et al., 2005). Site 11 is just inside the southern edge of a bay near the village of Kalalangabo. It is surrounded by steep, deforested slopes cultivated with cassava or used for grazing. The land cover of other sites is a mixture of agricultural and to a lesser extent developed lands.

Fish behavior

I assessed fish behavior by direct observations while snorkeling at the water surface. I observed 10 haphazardly selected fish (8 to 12 cm total length) at each site. Once I targeted a fish I waited for 20 to 30 second for the fish to acclimate to my presence, and I noted the time and began counting to 5. I recorded the behavior that the fish exhibited on the count of 5, and then resumed counting, again recording the behavior exhibited at the 5^{th} count. I continued this procedure for 10 minutes. The time activity budget include: 1) Feeding - the fish ingested periphyton, usually by orienting the head down and making contact with the rocky surface; 2) Swimming - the fish actively moved from one place to another; 3) Hiding - the fish disappeared under or behind a rock for less than 30 seconds; 4) Aggression – the fish attacked or was attacked by another fish, either a conspecific or another species; 5) Resting – the fish remained in the open but was not actively engaged in any other behavior. Based on preliminary observations in 2011, maximum feeding activity occurred from late morning to early afternoon. Therefore, in 2012, all direct behavioral observations occurred between 12:30 and 14:45. I observed fish at one site per day between 8^{th} July and 10^{th} August, 2012. The fraction of time spent in each behavior was calculated for each fish and a mean activity budget was calculated for each site.

I used video to determine the feeding rate (bites/minute) of individual fish and the duration of individual feeding bouts. Video data were collected while snorkeling at the surface between 10:30 and 12:00 immediately before the activity budget data were

collected. I used a Sony (model; CX 560) video camera in an Equinox ® housing. While slowly snorkeling through the site, I followed an individual fish until it disappeared from the camera view, after which I targeted another fish. The camera housing was bulky and it was necessary to continuously concentrate on video screen, making navigation through the site difficult. Therefore, observations of individual fish were typically of much shorter duration than the 10 minute direct observations described above. I continued to collect video for 1.5 h irrespective of the number of fish followed. Video recordings were viewed on a computer screen and analyzed by a single, trained observer. The moment a behavior appeared on screen, the video's timestamp was recorded along with the behavior. When the behavior changed, the video was paused, and a new behavior and initial time were recorded. Each fish was analyzed twice and the mean duration of behaviors was used for analysis. Behaviors were categorized as described above. Additionally, during each feeding event, number of bites or "pecks" the fish took at the rock was recorded. The duration of individual feeding events was calculated by taking the difference between the start time of the feeding and the time the next behavior began. Feeding rate (bites per second) was calculated for each feeding event and the average feeding rate was calculated for each fish.

I calculated a grazing pressure (bites/m^2/d) for each site using the following equation:

Grazing Pressure = TD x F x BPH x 8 hours

Where TD = *Tropheus brichardi* density (#/m^2, see chapter three, fish count at 12 sites between 0 to 8 m depth), F = the average proportion of the fish's activity budget devoted to feeding, and BPH is feeding rate (bites/h) (Fig. 2.7). I observed fish during the afternoon, when feeding activity was highest. Therefore we assumed an 8 h day for active feeding.

Fish morphology and diet

I captured sixty *T. brichardi* from < 4 m depth at each site using a gill net (one inch) between July 2nd and August 5th , 2013. I measured and weighed the fish (nearest 0.01 cm and 0.01 g respectively) to obtain information on the condition factor. During this time (30 to 45 min) all fish were held in a bucket containing clean lake water. After releasing (N=50) or sacrificing (N=10 fish) the fish, I concentrated the feces by decanting excess water, pipette and kept the feces in a 10 ml vials, which were then frozen for nutrient, AFDM and caloric analysis. The condition factor *K* is calculated as (Schneider et al., 2000):

$K = 100W/ L^b$, where W = weight of fish (g) and L = Total length of fish in cm, and

b = exponent obtained from fitting a by weight and length to a power function (Safran, 1992). An additional ten fish from each site were sacrificed and then kept on ice prior to dissection. In the laboratory before dissection, I recorded the weight (g) and Fork length (cm) of each fish. Fork length (FL) refers to the length of a fish measured from the

tip of the snout to the end of the middle caudal fin rays (Anderson and Gutreuter, 1983). Then I extracted the stomach contents by separating the food items from the stomach skin tissue. The stomach contents were weighed, transferred to glass vials and frozen for fatty acid analysis (n = 3 fish per site), C: N: P analysis (n = 3 fish per site) and algal composition assessments (n = 3 fish per site). I calculated stomach fullness of 10 individual fish as the weight of the stomach contents relative to the weight of the fish and computed an Intestine Length Index based on the length of the gut from stomach to rectum divided by fish fork length).

Stomach contents (N = 3 per site) were analyzed and compared with algal scrubs from the environment (see below) to test whether *T. brichardi* selectively feeds on specific algal groups. Algal suspensions from the fish stomachs and the periphyton on rocks were homogenized, subsampled (200 – 400□l), and filtered onto a Pall GN-6 Metricel® 0.45um mixed cellulose filter to achieve a concentration of approximately 20-30 cells per microscope field at 200X magnification. Filters were mounted permanently on glass slides using HPMA (2-hydroxypropyl methacrylate) resin (St. Amand). We counted algal cells on a Nikon Optiphot microscope (Nikon, Japan). To ensure proper identification of small cells and avoid double-counting of cells, we enumerated cells greater than 30 μm at 200X and smaller cells at 400X. At least 200 units (cells, filaments, or colonies) were counted at each magnification and identified by division (i.e., bacillariophyceae, chlorophyta, cyanobacteria). An average electivity index was calculated for each fish:

$E_i = (W_i - n^{-1})/(W_i + n^{-1})$ (Vanderploeg and Scavia, 1979),

where n = is the number of algal taxa available (3), and $W_i = r_i p_i^{-1} \Sigma(r_i p_i^{-1})^{-1}$. r_i is the percentage of a given taxon in the diet of the fish and p_i the percentage of the taxon item in the environment. E_i varies from -1 to 1. Negative values indicate avoidance, and positive values indicate active selection (Tofoli et al., 2013).

Periphyton composition

In 2013, divers collected cobbles (N = 4 per depth) from 1, 2.5, 5 and 7 m in order to measure chlorophyll a, Ash Free Dry Mass (AFDM), fatty acid content, and C:N:P. Cobbles were transported to shoreline and scrubbed within 1 hr. A quantitative periphyton sample was obtained by placing a 25.5 cm^2 plastic cap over a uniform portion of the upward facing side of the cobble. Periphyton outside the cap was removed with a wire brush and retained for ash free dry mass (AFDM) analysis. After removing the periphyton outside the cap, the quantitative periphyton sample was scrubbed from the rock surface, collected and centrifuged. The pellet was frozen in pre-weighed glass vials and then freeze-dried (Virtis equipment, Gardiner, NY) for subsequent analysis of chlorophyll-*a,* fatty acids and C:N:P

Periphyton P content was analyzed using the acid molybdate method for particulate samples (APHA, 1995). Duplicate subsamples (~ 5 mg) were combusted for 1 hour at 500 °C and then digested for 2 hours at 102 °C. After adding acid molybdate color reagent, absorbance was read at 880 nm on a micro plate reader (Bio-Tek Instruments,

Winooski, VT). Periphyton C and N content were analyzed with a Vario EL *I II* elemental analyzer (Elemental Americas, corporation, NJ, USA). Chlorophyll-*a* was analyzed by extracting subsamples in 90% buffered ethanol for 24 hours at 4°C in refrigerator and measuring fluorescence on a Turner Aquafluor fluorometer (2002). The proportion of organic matter (AFDM) in periphyton was obtained after combustion in a muffle furnace for 4 hours at 550 °C (APHA, 1995).

Total lipids were extracted from ~ 0.3 g of a lyophilized subsample using a ratio of 2:1 methanol: chloroform mixture (DeForest et al., 2012). We used the standard phospholipid 19:0 to determine lipid recovery. The phospholipid-derived fatty acids (PLFA) fraction was separated from total extracted lipids using silicic acid solid-phase extraction chromatography columns (500mg 6 ml^{-1}). The extracted phospholipids were converted to fatty acid methyl esters (FAMEs) and separated using a HP6890 GC-FID gas chromatograph (Agilent Technologies Inc., Santa Clara, California, USA). We identified individual PLFA using the Sherlock® Microbial Identification System (MIS) (MIDI, Inc., Newark, Delaware, USA). Response values generated from the Sherlock MIS were converted to a percent mole fraction of total PLFA.

Data analysis: Statistical tests were performed using the R- programming language software (R.2.15.2, Development Core Team,Vienna, Austria). We summarized fish behavior by using total activity budget (%), feeding rate (bites/sec) and feeding duration (time spent per feeding event).

Periphyton quality (% P, % N, %C, % organic matter, Chl a (mg/g), C:P and N:P) and quantity g/m2 (P, N, Chl. a, and sediments), were averaged in each site. I first calculated a mean for each depth and then for the site. I used periphyton data only from 1 and 2.5 m depth to correspond to the habitat that the fish occupied. Since we had eleven diet parameters, PCA is used to identify the minimum sets of predictors (periphyton composition) which were likely to explain the differences in feeding behavior among sites.

The first two principal components explained 71.5 % of the variance in chemical composition (see results). I used regression analysis to assess the influence of algal composition (PC1 and PC2) on the proportion of the afternoon activity budget devoted to feeding activity, the duration of individual feeding events (time/patch) and the feeding rate (bites per sec) during individual events. The relationship between fish density, condition factor and stomach fullness was assessed using one-way ANOVA. I also regressed periphyton quantity (PC1), quality (PC2) with the intestinal length index.

2.4 Results

Periphyton composition: Periphyton quality and quantity varied among sites and metrics of quality related to elemental compostion of periphyton were highly correlated. The first two components (PC1 and PC2) accounted for 71.5 % of the variance (Fig.2.1). The PC1 axis had highest loading for organic matter (g/m^2), which is an index of food quantity, and inorganic sediments (g/m^2). The correlation between PC1 and organic mater and

sediment was 0.96 and 0.98 respectively. The PC2 axis had the highest loadings for periphyton chlorophyll concentration (mg/g) and % P which are indicators of food quality. Most sites were distributed along a gradient of low quantity with high quality to high quantity with low quality (Fig. 2.1). Site 13 was an anomoly in that it had high quantities of high quality algae and high sediment accumulation. We ran several of the regression analyses both with and without site 13 because it was often an outlier.

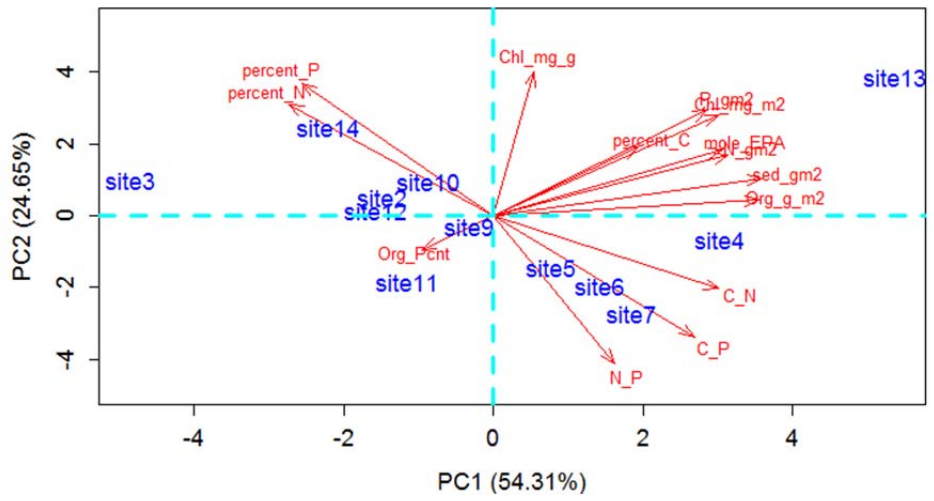

Figure 2.1: The PCA results for periphyton quality and quantity at each site; data collected from Lake Tanganyika, in 2013. PC1 represents food quantity g/m^2 (organic matter, and sediments) and PC2 represents food quality (% P and chl mg/g). Dashed lines separate high and low values.

Fish behavior: Between 12:30 and 14:45, *T. brichardi* spent 98% of their time actively foraging, which included feeding on algae and swimming. There was an inverse relationship between swimming and feeding but there was no signigficant effect of site (Fig.2.2). Fish spent little time (0.06%) engaging in agonistic behaviors, such as attacking or being attacked by conspecifics or other species. Hiding and resting comprised 1.4% of the total time**.**

The percentage of feeding activity that a fish at a given site devoted to feeding varies among sites, and between two replicates (at each site fish behavior was done twice with an interval of one week between the two replicates; $p < 0.05$), and was marginally

negatively related to food quantity (PC1) and negatively and siginificantly related to food quality ($F_{(1,115)} = 27$, Fig. 2.3, Table 2.1). PC1 incorporated both inorganic sediments and organic matter, which were positively correlated ($r = 0.98$, $p = 0.05$). Thus, as organic matter and sediments increase fish increase their swimming activity, probably searching for food.

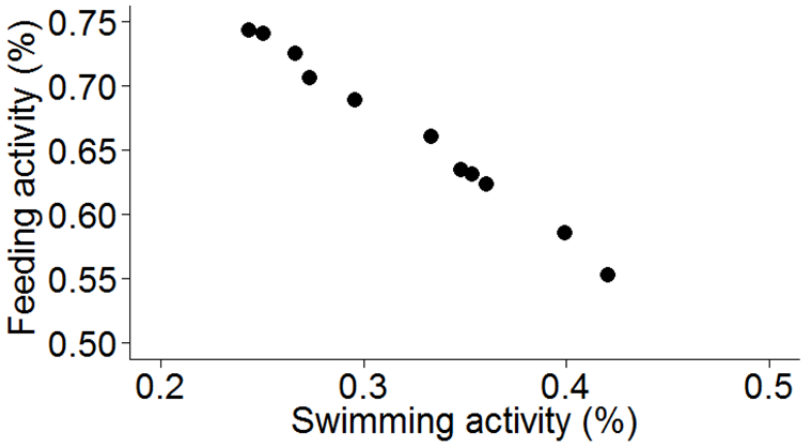

Figure 2.1: Relationship between feeding and swimming activities budget of *T.brichardi;* Fish spent little time engaging in agonistic behaviors, hiding and resting which comprised 2% of the total time; data collected between June and August, 2012. Each point represents a site (n=11).

The average duration of individual feeding events per patch differed among sites ($p < 0.05$), ranging from 14 to 92 seconds per patch. Time per patch also negatively related to PC1 ($F_{(1,316)} = 15$, $p < 0.05$) and positively related to PC2 ($F_{(1,316)} = 5$, $p = 0.02$, Table 2.1). Thus, individual feeding events lasted longer when both organic matter and

sediments were low and when periphyton quality was high. The interaction between PC1 and PC2 was not significant. Feeding rate (bites/sec) during a feeding event varies among sites ($p < 0.05$). However, there was no relationship between feeding rate and periphyton quantity (PC1) or quality (PC2) ($p > 0.05$; Table 2.1).

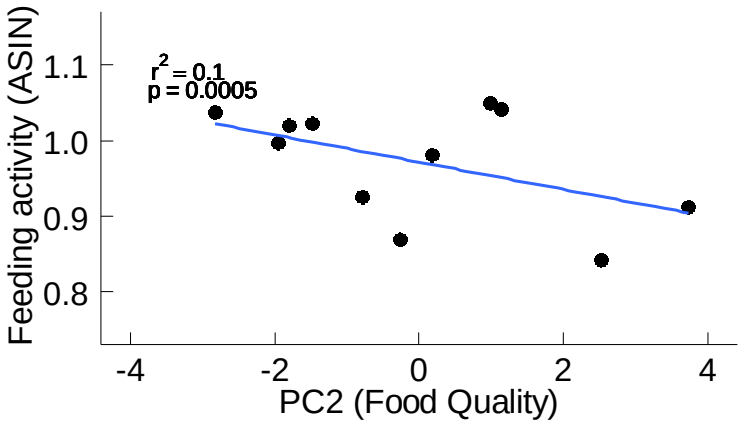

Figure 2.2: Regression between feeding activity (ASIN-Transformed) and food quality (PC2). Data collected between June and August, 2013.

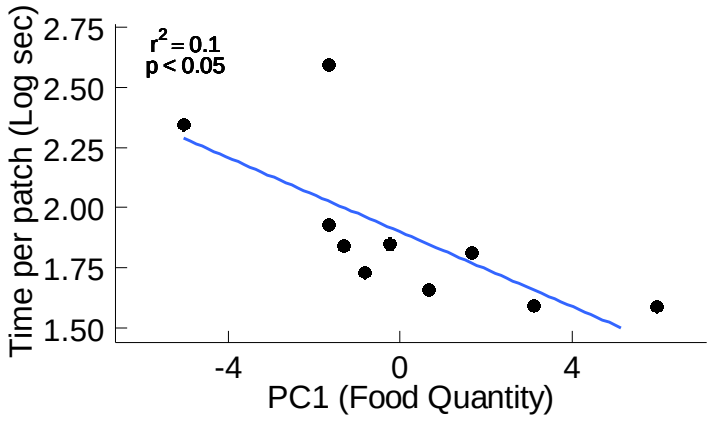

Figure 2.3: Regression between times spent feeding per patch (Log-Transformed) and food quantity (PC1). Data collected between June and August, 2013.

The relationship between algae from the environment and that in the fish fut indicated that cyanobacteria and green algae had a wide range among sites than diatoms. However, chlorophytes and green species were rare in the environment as well as in fish guts (Fig. 2.5). Regarding the complex nature of the feeding behavior of *Tropheus* and variation in algae community due to variation in environmental factors it was necessary to calculate the selectivity index, which provided some information on fish's food preference. According to Vanderploeg and Scavia, (1979) equation, fish at all sites demonstrated a high selectivity for diatoms relative to other algal species (Fig. 2.6). This result indicates that, *T. brichardi* did not consume food at random but have the ability to select and choose the preferred foodstuff.

Daily grazing pressure (expressed as bites/m^2/day) ranged from 5000 to 13000 among sites. High grazing pressure significantly decreased periphyton biomass (organic matter), ($r^2 = 0.68$, $p = 0.008$; Fig. 2.7), but site 13 was omitted as an outlier with both high grazing pressure and high fish density.

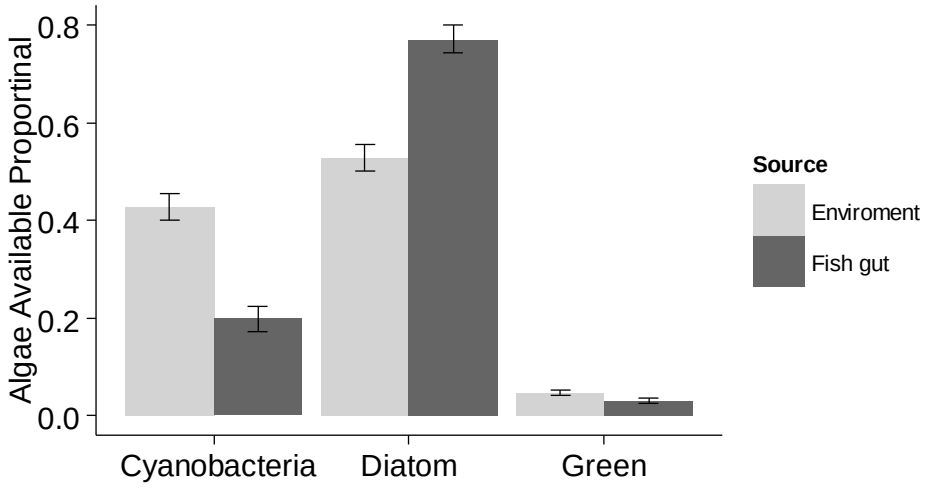

Figure 2.4: Proportion of algae species from the surrounding environment and fish gut-stomach (n = 74); data collected between June and August, 2013. Error bars represent standard error of the mean.

Table 2.1: Regression results showing the influence of periphyton food (quality and quantity) on feeding activities (%), time spent feeding per patch, feeding rates, intestine length index, stomach fullness index and condition factor, data collected June – August, 2012 - 2013. Significant effects are marked in boldface type.

Response	Slope	Df	SS	MS	F value	P value
Feeding rep 1 (6 sites; 10 fish)						
Quantity (pc1)	-0.01	1	0.028	0.028	2.886	0.0928 .
Quality (pc2)	-0.02	1	0.129	0.129	13.145	**0.0004***
Quantity *Quality	0.005	1	0.051	0.051	5.246	**0.0231 ***
Error		106	1.043	0.009		
Time spent per bout (10 sites;17 -54 fish)						
Quantity (pc1)	-0.08	1	14.564	14.564	25.014	**< 0.05**
Quality (pc2)	0.06	1	2.847	2.846	4.889	**0.0277 ***
Quantity *Quality	-0.003	1	0.057	0.057	0.098	0.7542
Error		317	184.576	0.582		
Bites per sec (10 sites;17-54 fish/site)						
Quantity (pc1)	0.006	1	0.5	0.5	2.318	0.129
Quality (pc2)	0.026	1	0.551	0.551	2.552	0.111
Error		316	68.199	0.216		
Intestine Index (12 site; 10 fish,)						
Quantity (pc1)	0.041	1	1.397	1.397	6.131	**0.014 ***
Quality (pc2)	-0.027	1	0.253	0.253	1.112	0.294
Error		116	26.435	0.228		
Log-stomach index (12 site; 10 fish)						
Quantity (pc1)	-0.011	1	0.13	0.13	0.295	0.588
Quality (pc2)	0.016	1	0.112	0.112	0.255	0.614
Error		112	49.275	0.44		
Condition factor (10 fish,12 site)						
Quantity (pc1)	0.004	1	0.013	0.013	0.225	0.636
Quality (pc2)	0.027	1	0.311	0.311	5.558	**0.020 ***
Error		116	6.487	0.056		

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

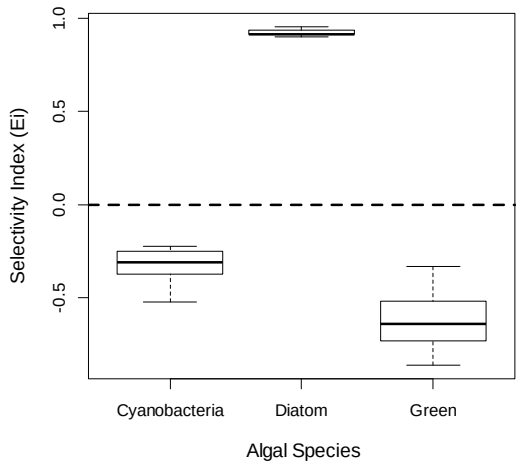

Figure 2.5: Feeding selectivity index (E_i) of *Tropheus brichardi* for different types of algae in Lake Tanganyika, (n = 74); Cyanobacteria and Green algae had a wide range among sites than diatoms. Data collected between June and August, 2013.

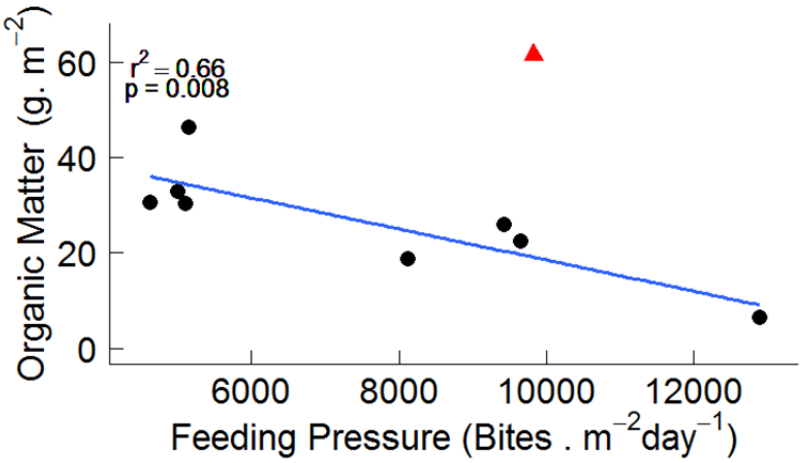

Figure 2.6: Relationship between organic matter (gm^{-2}) and feeding pressure (bites $m^{-2}day^{-1}$). Each data point represents a site. Data collected from June - August, 2013. Feeding pressure was calculated as feeding rates (bites sec) * % feeding activity *fish density (#/m2). Site 13 (indicated by a triangle) was an outlier.

Stomach fullness (stomach weight/fish weight) ranged from 0.008 to 0.06 with a mean of 0.016 ± 0.002 (mean ± SE). Periphyton quantity (PC1) and quality (PC2) did not affect the stomach fullness of *Tropheus* (Table 2.1). Mean intestine length relative to body length (ILI) ranged from 4.4 to 5.2 and differed significantly among sites ($p < 0.05$). Site 4, 5, 6, 7 and 13 had the highest ILI and site 11 had the lowest ILI. Regression results indicated that fish at sites with high quantity (sediments and organic matter) had longer ILI (Fig. 2.7; Table 2.1) compared to fish at sites with low quantity (PC2). Our results also reveals a positive relationship between PC2 (periphyton quality) and condition factor (Table 2.1).

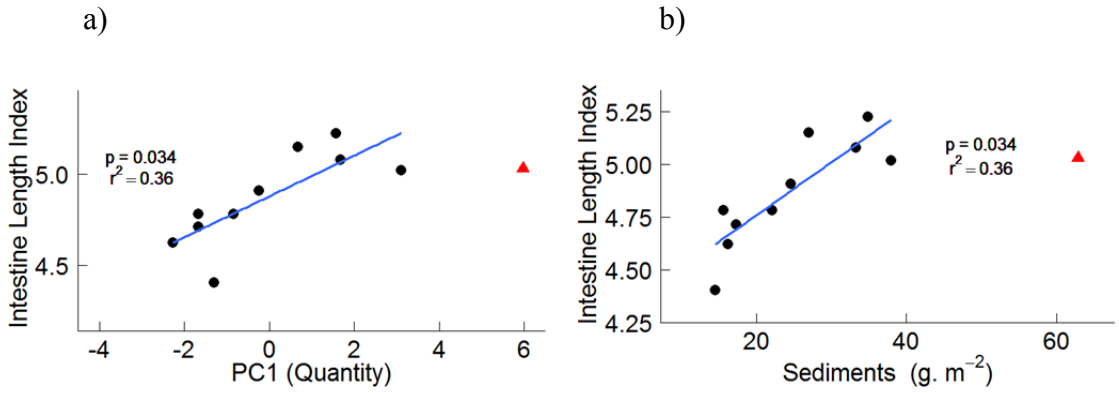

Figure 2.7: Relationship between (a) Intestine length index and periphyton quantity (PC1). (b) Intestine length index and sediments. Each data point represents a site; data collected June - August, 2013. Site 13 (indicated by a triangle) was an outlier was omitted in regression analysis.

2.5 Discussion

Tropheus fish feed on periphyton by biting and tearing off epilithic algae growing on the surface of the rocks. The quality and quantity of periphyton vary with environment which requires algivores to make decisions about where they want to feed, when to feed,which food type to select, and how long they have to stay and feed in a patch. Our results show that, *Tropheus* feed selectively on high quality food in order to maximize energy and nutrient intake. An increase in intestinal length and size observed in this study, has been assumed to facilitate a more efficient utilization of poor food associated with sediments because larger guts have higher surface area and allow longer food transit times, which enhance nutrient and energy absorption (Sibly, 1981).

Behavioral responses to among-site variation in resource quantity and quality

The marginal value theory (MTV) predicts that animal should stay feeding in a patch as long as there is a maximum energy gain or maximum food intake per unit time (McNair, 1982). When an animal starts feeding in a patch, the energy gain per time starts to decrease because food diminishes with feeding time in a patch and the marginal value (amount of food remaining per patch) decreases as the patch is exploited. Our results reveal that as the quantity of sediment and organic matter increases (PC1) fish decrease their feeding activities while increasing their swimming activity, most likely searching for food. There are many problems associated with sediment in the aquatic environment, sediments dilute and cover periphyton (Donohue and Garcia, 2009; McIntyre, et al 2005),

making food more difficult to obtain. In order to maximize energy intake, as the amount of sediment decreases, *T.brichardi* increased handling time by increasing their feeding activity while reducing the swimming and searching costs. This pattern was also found in other species (Doran, 1997; Agetsuma and Nakagawa, 1998). Our study reveals that sites with high sediments, caused fish to decreased the feeding activity and increasing the swimming activity probably looking for food. Sediment dilutes algal food and makes it difficult to find, as a result fish may has to spend more time searching for food. However, searching may increase the energy expenditure which might affect energy availability for growth and other activities.

Fish spent more time feeding in a high quality patch when there was high quality food with low sediments. While foraging on a patch, *Tropheus* are likely to sample their environment in order to collect the information needed to trigger the patch leaving decision (Wajnberg et al., 2000; Yamada, 1988). Patch quality is defined as a function of net energy gain and for this study is determined by food quality and availability. The short stay in sites with sediments (PC1) observed in this study, may reflect a non-preference to feed in sediments patches due to the negative rewards associated with sediments. Sediment increased the handling time to obtain the food, and therefore higher costs to foraging. The decision when to leave a depleting patch depends on expectations of potential patches which include intake rates and travelling time between patches. If the travelling time to a new area is long, fish will prefer to stay and feed in the current area until the area is depleted quite severely before it become advantageous to abandon it.

However, *Tropheus* fish are territory (Hermann et al., 2015) these fish don't move far away from their territory. Our results support the predictions generated by the Marginal Value Theorem (Cowie, 1977; Naef-Danenzer, 1999), that fish spend more time feeding in high quality patches in order to maximize energy intake per unit time. While the fish is feeding within a patch, it experiences the law of diminishing returns (Davis, 1975), where it becomes harder and harder to find a prey as time goes on. This may be because the prey is being depleted especially when it is being covered by sediments. Energy gain is presumably lower in the sediments sites because of the dilution factor. To meet their energetic need, the fish in sediment sites has to spend less time feeding in each patch, then swim for a while, then feed again. Fish have to gain the most benefit (energy) for the lowest cost during foraging, so that it can maximize its fitness which includes growth, reproduction and survival which needs energy.

The problems associated with poor quality food can potentially be avoided by selection of higher quality food items which contain substantial amounts of easily digestible lipids, carbohydrates, and protein (Linton and Greenaway, 2007). *T. brichardi* feed selectively on diatoms. Diatoms were found to contain high content of EFA (Brett and Müller-Navarra, 1997; Wichard et al., 2007; John et al., 2001; Ying et al., 2000), which is the key factor that determines food nutritional quality, perhaps indicating that the fish were optimizing both nutritional value as well as energy consumption because fatty acids are the source of adenosine triphosphate (*ATP*) when burned. Moreover, the digestive ability of diatom is very high than that of cyanobacteria. Hence, the fish might

be looking for algae with highly digestible. Essentially, while feeding, *T. brichardi* also pick a small proportion of green algae (intermediate quality), and cyanobacteria (poor quality) (Müller-Navarra et al., 2000, Brett and Müller-Navarra, 1997). The presence of non-profitable diet items (e.g Green algae and cyanobacteria) may provide essential nutrients and nitrogen which are not present in adequate amounts in the basic diatom diet. The basic optimal foraging theory predicts that organisms should always choose the most profitable prey available (Pyke, 1984), and they should selectively ignore less profitable prey when the most profitable prey occurs at or above a certain level. However, this is not always true. A study on birds revealed that birds cannot discriminate between high and poor quality when the density of both were low, and they ignored the less profitable prey only when the density of the more profitable prey was very high, (Krebs et al., 1977). The presence of blue green and cyanobacteria in *T.brichardi* stomach suggests that the herbivores may have difficult in making perfectly optimal foraging decisions; without perfect knowledge, a predator's behavior cannot be perfectly optimal (Frens, 2010).

When faced with poor quality food, in order to maintain high growth rates, high reproduction, and high survival rates *T.brichardi* have to compensate for the poor food quality by feeding at higher rates or for longer periods on food of inferior quality (Reynolds 1990, Wright et al., 2003). However, our result does not show any compensation activities because fish in poor quality sites, reduced their foraging efficiency by decreasing their feeding rates and time spent feeding per patch while increasing their swimming activities. This increase in swimming activity may increase

metabolic costs or energy expenditure (Schreck, 2010), that is reflected in an increase in oxygen consumption.

Grazing pressure

High feeding rates may affect food availability especially when there is high fish density. High grazing pressure can lead to the formation of small heterogeneous grazing patches, as animals repeatedly select the accessible and the most palatable plant (Launchbaugh, 1996) with high nutritional value and leaves chemical or structural defenses (McNaughton, 1980). In this study, low grazing pressure in sediment sites resulted into high EFAs in periphyton compared to highly grazed sites which had low sediments.

The steady decrease in organic matter with increase in grazing pressure that was observed in this study is a typical response in previous grazing studies. Significantly lower biomass in the highly grazed sites suggests negative effects of grazers on algae (Hunter et al., 1997; McIntyre et al., 2006; Miller et al., Nyanza project, 2005). Response of benthic periphyton to grazers involves a variety of community population response that may vary with grazing intensity and nutrients level. Grazing pressure may also influence algal production because benthic algal growth is commonly limited by the availability of nutrients. Our results also revels that the combined effects of lower algivore densities (chapter 3) and lower feeding rates along a gradient of sediment accumulation led to a decrease in grazing pressure at high sediment sites. Sediment

covers and dilutes algae, thus deplete the algal quality. This may increase the digestion costs to herbivores; consequently, produce negative cascading effect through the food chain. The positive relationship between fish conditon factor and food quality suggest that high food quality enhanced fish fitness.

Morphological responses to among-site variation in resource quantity and quality

Tropheus are able to efficiently utilize periphyton food by possessing a plastic digestive strategy which involves increase in intestine and stomach size to increase the intake of high quantities of low quality food. The positive and strong relationship between intestine length index (ILI) and food quantity (sediments and organic matter (g/m^2)) may be a result of a trade-off between maximum nutrient absorption and cost minimization (Sibly, 1981). The presence of sediment in periphyton negatively affects both quality and quantity (McIntyre, 2005). Sediments dilute algae and lower the relative abundance of algae (Gilbert, Nyanza project, 2005). A change in digestive tissues in response to a change in food quantity is a classic example of reversible phenotypic plasticity (Olsson et al., 2007; Piersma and Lindström, 1997; Wagner et al., 2009). The optimal digestion theory suggests a tight link between the morphology of the digestive system and food quality and quantity (Sibly, 1981). Phenotypic plasticity is advantageous for herbivores because it enables them to efficiently utilize plant material since longer guts have higher surface area and allow longer food transit times that enhance nutrients and energy absorption (Sibly, 1981; Troyer, 1991).

Tropheus brichardi are classified as browsers (Horn, 1989), and the feeding strategy is to bite and tear upright algae, and they rarely ingest sediments during feeding. However our data revealed high amount of sediments in feces (45%) and the correlation between sediments in the environment and that found in the stomach was positive but not significant (Renalda unpublished data).

In conclusion, our results reveal that in a short term, *T.brichardi* are able to modify both feeding behavior and gut morphology to reflect changes in food quality and a reduced food availability. In the presence of poor food diet, *T.brichardi* compensated by feeding selectively on diatoms which contains high essential fatty acids and decreasing the time spent feeding per bout. On the other hand the presence of sediments resulted in high swimming activities probably searching for food and an increase in ILI. The increase in relative intestinal length index (ILI) may facilitate a more complete extraction of nutrients and energy. This study was able to assess a short term effects of sediment and poor quality food on *Tropheus,* However, further research should be conducted to understand the impact of sediments and poor food quality on *Tropheus* fish in a long-term scales

CHAPTER THREE

Herbivores distribution within and among sites in Lake Tanganyika varies with food nutritional quality and quantity.

3.1 Abstract

The concentration of nutrients in primary producers affects both the growth rate of primary consumers and the proportion of ecosystem primary production that is channeled into herbivores as opposed to detrital trophic pathways. There is a logical intermediate step between high food quality causing high primary consumer growth rate and nutritious primary consumers generating strongly inverted trophic structure at the ecosystem level that has not been demonstrated within an ecosystem: The herbivore carrying capacity of a habitat should be positively correlated with primary producer nutrient content (food quality) rather than primary production (food quantity). The basic model posits that algae with high nutrient concentrations yields higher growth rates per unit of primary production consumed which in turn increases herbivore density within a habitat. I assessed fish density, algal quality and quantity along an inshore-off shore gradient at 12 sites to provide for within and between site comparisons. I used regression analysis to determine the relative importance of depth, algal quality and quantity in influencing the distribution and condition factor of algivorous fish. Within sites, algivores density, and periphyton quality and quantity all decreased with depth a pattern consistent with fish

maximizing caloric and nutrient input by aggregating in shallow areas. Among sites, algivores distribution was positively correlated with food quality, uncorrelated with algal productivity, and negatively correlated with algal biomass, patterns that indicate a strong bottom up and top-down effects of fish on algae. The among-site pattern is consistent with a strong effect of the fish on both algal biomass and nutrient content. However, the positive correlation between fish densities and algal quality across sites may also reflect a positive effect of food quality on the carrying capacity of different habitats within the lake. Although fish production of Lake Tanganyika is comparable to harvests from marine ecosystems, a driving force of having such a high biomass is not the presence of habitat complexity; rather it was high periphyton quality. In Lake Tanganyika habitat complexity had no significant influence on the likelihood of grazers being present and the relationship was negative. We conclude that littoral nutritional quality influenced fish distribution.

3.2 Introduction

The palatability and food quality of primary producers strongly influences ecosystem structure because the nutrient content of primary producers determines whether carbon fixed by autotrophs is consumed as living tissue by herbivores or whether it is shunted through detritivore pathways (Cebrian, 2002). Ecosystems in which primary producers have a high nutrient content have high ratios of herbivore biomass to autotroph biomass (Cebrian et al., 2009). High autotroph palatability leads to strongly inverted trophic pyramids and high efficiency of energy transfer from primary producer to herbivores. Across terrestrial and aquatic ecosystems, micro-algae have the highest food quality and lowest C:N:P of any primary producer (Cebrian, 1999, Sterner and Elser, 2002). Nevertheless, within aquatic ecosystems algal quality varies based on taxonomic composition, grazing pressure and the availability of nutrients relative to light (Sterner et al., 1997; Liess and Kahlert, 2007).There is a plethora of evidence demonstrating the correlation between algal quality and consumer growth rates (Elser et al., 2000, Sterner 1993; Sterner and Hessen, 1994), but it is less clear that algal quality, rather than algal production, determines the carrying capacity of algivores at local or landscape scales. Globally, eutrophication and increased terrigenous sediment loading are transforming shallow water marine and freshwater ecosystems often causing dense growths of attached algae. Despite a positive effect of nutrients on quantity of their algal food, algivorous fish appear to be particularly vulnerable to these anthropogenic stresses (Cohen et al., 1993).

Although the trophic basis of ecology focuses on energy flow between trophic levels (Lindeman, 1942; Oksanen, 1988), the growth and abundance of primary consumers can shift between limitation by caloric intake and nutritional content of their primary producer food (Gaedke et al., 1996). Spatial variation in the quality of primary producers can be generated by variation in bottom up drivers such light and nutrients (Sterner et al., 1997) as well as in response to top-down control by the grazers themselves (Frost, 1987; McIntyre et al., 2006). The emergent combined effects of variation in food nutrient concentration and food quantity on the distribution of primary consumers are difficult to predict at habitat or ecosystem scales. Within habitats, primary consumers can rapidly respond to spatial variation in food by aggregating in highly productive areas to maximize carbon or nutrient acquisition (Power, 1984; Anderson et al., 2010). Among isolated habitats or ecosystems, variation in primary consumer abundance is expected to reflect the realized accessibility of the nutrient pool to primary consumers (Gaedke et al., 2006; de Mazencourt et al., 1998). If food palatability and carbon to nutrient ratios affect the accessibility and digestibility of primary producers, then grazer densities may depend more on food quality than nutrient standing stock or primary productivity.

Algivorous fish (algivores) dominate fish biomass and diversity in marine and freshwater tropical ecosystems. The density and spatial distribution of algivores within a habitat are determined in part by the availability (quantity) and spatial distribution of food (Power, 1983). However, relating algivore abundance to food availability at any spatial scale is confounded by the extremely strong top down control that algivores exert

on their resource. Algivores substantially reduce microalgal or macroalgal biomass (Burkepile and Hay, 2009; Power, 1990; Flecker et al., 2002) making steady-state measures of algal standing stock an ambiguous metric of resource availability in heavily grazed ecosystems. Indeed, a hallmark of strong top down control is that increases in autotrophic productivity are manifest as an increase in consumer, rather than autotrophic biomass (Power, 1992). Although the more informative algal productivity is measured much less often than algal biomass density, the limited data demonstrate that algivore abundances closely track area-specific algal productivity as determined by light (Power, 1983, 1984, Connell and Jones 1991; Hori, 1983). Thus, food availability (quantity) determines algivore distribution at the local scale, although predation threat can modify grazing behavior (Lima and Dill, 1990).

Algivores selectively feed on algae with high nutrient concentrations, but there is currently no evidence that algal quality affects the carrying capacity of habitats. Food quality, including nutrient concentration (C:N:P) and fatty acid content, strongly affect the growth rates of primary consumers across phyla (Sterner and Elser, 2002; Müller-Navarra et al., 2000). Extremely high carbon to nutrient ratios or low essential fatty acid concentrations can substantially diminish growth and survival of primary consumers (Müller-Navarra, 1995). Despite the well-established theoretical and empirical links between food quality and primary consumer growth, few studies have correlated primary consumer distribution with primary producer nutrient concentrations at either local or landscape scales (Anderson et al., 2010). If algivore growth is limited by nutrient rather

than carbon acquisition, and if there is a substantial metabolic cost to consuming algae with poor nutritional content, then habitats with high concentrations of N and P in the algae should support higher densities of algivores.

Do habitats with higher food quality support higher densities of primary consumers and if so, is this pattern decoupled from primary productivity (food quantity)? The fish fauna of shallow rocky wave zone in Lake Tanganyika is dominated by aggressively territorial algivores that have relatively stable year to year populations (Hori et al., 1993; Takeuchi et al., 2010, McIntyre unpublished data). Individual rocky habitats are separated by expanses of sand that impose a dispersal barrier to algivores specializing on algae attached to rocks. Within rocky habitats, algivore territory size increases with depth in response to declines in the productivity of the algal food (Christian, 2008; Hori et al., 1991). However, there is there is also 4-fold variation in algivore densities among isolated rocky habitats (sites) within a 15 km stretch of shoreline (McIntyre unpublished data). We characterized within and among habitat variation in algivore densities in relation to both food quality (C:N:P) and quantity (algal productivity). Littoral algae are strongly light limited (Vadeboncoeur et al., 2014), and we expected that the rate of carbon fixation (food quantity) would decreases with depth within habitats. In contrast, the light nutrient hypothesis (Sterner et al., 1997) predicts that food quality, assessed as C:N or C:P , would increases with depth. Thus, changes in algivore densities with depth within a given site should reflect the optimal rate of supply of carbon relative to nitrogen and phosphorus. Among-site, variation in exposure to upwelling (Corman et al., 2010),

anthropogenic nutrients (Kelly et al., in prep), and sediments is expected to drive variation in attached algal productivity and nutrient concentration.

3.3 Methods

Study site: Lake Tanganyika is an ancient tectonic lake in East Africa and is the world's second largest freshwater lake by depth and volume (Herendorf, 1990). Water column dissolved nitrogen and phosphorus concentrations are near detections limits, and the euphotic zone (>1% surface light) extends to over 60 m. The lake's shoreline is composed primarily of rocky bedrock outcrops interspersed with expanses of sand (Cohen et al., 1993). A guild of algivorous fish in the tribe Tropheini dominate the littoral zone fish assemblage and specialize on the diatoms and cyanobacteria that grow attached to the rocks (Hori et al., 1991). I quantified the distribution of algivorous fish and their attached algal food resource in the rocky littoral zone during the dry seasons (June – August) of 2011, 2012 and 2013 (Table 3.1). I monitored algivores and their food at 12 spatially isolated sites (> 1 km shoreline between sites) along 15 km of shoreline in the Kigoma region of Tanzania (Appendix A).

We selected sites across a gradient of land use and wave exposure, two variables that are likely to affect nutrient and sediment retention in the shallow littoral habitat. Three southern sites (sites 2, 3, and 4) around Jakobsens beach resort and the

southernmost site (13) at Kitwe point are bordered by Miombo forest mixed with grass, but experience a gradient of wave action depending on shoreline orientation to the prevailing winds. Site 6, near the village of Katabe, is protected from wind and wave action and surrounded by sparse grassland. Site 7 was located in a protected bay with a very low slope and was obviously degraded by sediment from a hotel located at the top of an overhanging cliff (McIntyre et al., 2006). Site 11 is just inside the southern edge of a bay near the village of Kalalangabo. It is surrounded by steep, deforested slopes cultivated with cassava or used for grazing. The land cover of other sites is a mixture of agricultural and to a lesser extent developed lands (Appendix A; Table 3.1).

Table 3. 1: Site coordinates with latitudes and longitude and a slope calculated at 0 to 3m depth from the main shore, for the data collected in June to August, 2011, 2012 and 2013.

site Id	site name	Latitude 4° S	Longitude 29° E	Hypotenuse from the shoreline to 3 m depth
2	Jacobs Outer	54.984	35.758	5.787-cliff
3	Jacobs Inner	54.805	35.898	9.407
4	Jacobs North	54.515	35.805	14.090
5	Maji Menge	54.154	35.678	21.994
6	Katabe South	53.999	36.044	21.448
7	Katabe North	53.671	36.740	30.105
9	Nandwe Point	51.763	36.498	15.249
10	Euphorbia	50.959	36.514	10.618
11	Kalalangabo South	50.611	36.468	11.153
12	Kalalangabo North	50.214	36.523	15.474
13	Kitwe Point	55.203	36.691	21.203
14	Kagongo South	49.572	36.260	13.692

Fish: In 2011, we conducted visual surveys of 2 algivore species (*Tropheus brichardi* and *Petrochromis kazumbe*) from 0 to 8 m depth. At each site, divers deployed 3 marked transect lines that ran parallel to the slope of the lake bottom. The 3 lines were spaced 5 m apart and extended from the lake edge (0 m) to a depth of 8 m. A diver placed markers along the lines at 0.5,1, 2, 3, 4, 5, 6, 7, and 8 m depth. The 3 lines delineated two 5 m wide quadrats that were divided into 9 depth intervals of variable surface areas. The horizontal length of each depth interval was measured during habitat complexity measurements (see below). After deploying the lines, the quadrats were left undisturbed for 20 minutes before counting began.

I snorkel slowly drifted from the shore to 5 m counting all individuals of *T. brichardi* and *P. kazumbe* at each depth interval along the transect line. Scuba was used to census fish between 5 m to 8 m with the diver maintaining a vertical distance approximately 3 m between her and the lake bottom. Each quadrat was censured twice with 30 to 45 minutes between samplings. Duplicate counting of individual fish was minimized by drifting along the transect line in a single direction and counting fish as they appeared in the counter's field of view from downslope. Fish density at each depth, within each transect, was calculated by averaging the two counts and dividing by the planar surface area of each depth interval. The majority of fish in the 2011 survey occurred between 0-3 m. Therefore, in 2013 three 5-m wide quadrats were deployed from 0-3 m. Only *T. brichardi* was counted in the 2013 survey.

In addition to the algivore counts, we visually censured each site's entire fish community once per year. Counts were made around midday, and 1-2 sites were censured on any single day. A snorkeler (McIntyre) deployed three 7 x 8 m rope quadrats at each site. Quadrats were oriented perpendicular to shore, with the deep margin at 5m and the shallow margin varying between 2-4 m depth depending on the bathymetry of the site. Quadrats were separated by 5-10 m along the shoreline. After deployment, no one swam near the quadrat for at least 30 minutes before counting commenced. Fish were identified to species and counted by the snorkeler drifting slowly across the quadrat at the surface. The most skittish species were counted first. After counting all mid column fish, the snorkeler made a series of successive dives to count benthic species within the entire quadrat. This method provides a minimum estimate of fish densities and diversity within a known area.

Sixty *T. brichardi* were captured from each site using a two inch gill net during the dry season (July-August) in 2011, 2012 and 2013. Each fish was measured (nearest 0.01 cm) and weighed (nearest 0.01 g). Fish were held in clean lake water until all individuals were measured. We then siphoned the feces from each bucket, kept in glass vials. Samples were frozen for nutrient and caloric analysis. Each year, ten fish from each site were sacrificed and dissected. We measured gut length (stomach to rectum), and stomach fullness (expressed as the weight of the stomach contents over the weight of the fish) on each sacrificed fish. The stomach contents of each fish were separated from

stomach tissue and frozen for fatty acid analysis (N= 3 fish per site) or C: N: P analysis (n = 3) fish per site.

We calculated the condition factor of each fish by fitting weight and length to a power function (Safran, 1992), $W = aL^b$, where W = weight of fish (g) and L = Total length of fish in cm. After solving for the exponent b, the condition factor *K* is calculated as (Schneider et al., 2000):

$K = 100W/ L^b$ $\quad Eq. 1$

The factor of 100 brings K close to unity. Weight-length relationships were calculated for three years from 2011, 2012 and 2013. The relationship of condition factor as a function of fish density was estimated using data from 2013.

Rugosity: We measured 3 dimensional habitat structures of each site in 2011. We used the three transect lines that demarcated the fish census quadrats. The first depth interval was from 0 to 0.5 m and each subsequent depth interval corresponded to a 1 m change in vertical height (V) along the lake bottom. The planar horizontal distance (H) was measured by holding a tape measure parallel to the lake surface and measuring the horizontal distance between depth z and depth z+1. Divers laid a heavy chain along the contours of the lake bottom next to the transect lines between within each depth interval. We recorded the total length of chain that was needed to reach from depth z to z+1. Using the horizontal and vertical (depth) distances as two sides of a right triangle, we calculated the hypotenuse as the minimum distance along the lake bottom (hypotenuse) in the

absence of surface roughness. The habitat index was calculated as a ratio between a chain length and the hypotenuse (McCormick, 1994). Three habitat complexity transects were taken perpendicular to the shore at each site.

Attached algae: Variation in primary productivity as a function of depth was monitored at each site using PAM fluorometry in 2012. Photosynthesis-irradiance curves were monitored along 2-3 depth transects at each site. Each transect consisted of Rapid Light Curves (RLCs measurements at 0.5, 1, 2, 3, 4, 5, 6, 7, and 8 m. The fiber optic cable of the PAM was fixed 5 mm above the substrate in an opaque holder. A diver placed the fiber optic light assemblage over horizontally oriented rock surfaces and waited 20 s before beginning a RLC in which the algae were exposed for 10 s to each of 9 sequentially increasing light intensities. The diver collected the PAM data between 10:00 and 14:00 at each site. We used SAS Proc NLIN to solve for $rETR_{MAX}$ and □ □using the hyperbolic tangent function of Jassby and Platt (1976):

$$rETR = rETR_{MAX} tanh \frac{\alpha E}{rETR_{MAX}} \qquad Eq. 1$$

where *rETR* is relative electron transport rate at light intensity *E*. Proc NLIN converged on a solution in fewer than 15 iterations for all PE curves.

Among site variation in attached algal (periphyton) primary productivity was measured in situ in 2012 using bulk oxygen exchange methods **(**O'Reilly, 2000; Vadeboncoeur et al., 2014; Devlin et al., 2015). In brief, five clear (light) and 5 opaque (dark) open-bottomed acrylic chambers were deployed on rock surfaces at 2.5 m and 5 m.

Chambers were secured to rocks by placing a lead collar over a neoprene skirt that extended from the bottom edge of the chamber. Water was sampled from each chamber immediately upon deployment using a needleless 60 cc syringe. An internal paddle was used to manually mix water within the chamber before each sample was drawn. Immediately after withdrawing the sample syringes were sealed with a rubber cap. Final water samples were withdrawn from the ports after 20 minutes (light) or 2 hours (dark). Capped syringes were kept at lake temperature (< 30 minutes) until O_2 measurements were made with a YSI ProODO oxygen meter. The bore of the syringe was quickly and carefully removed and the oxygen probe was inserted directly into the syringe. We calculated area-specific gross primary production (GPP) as the sum of oxygen produced in the light chambers and consumed in the dark chambers. We converted GPP to carbon equivalents using a photosynthetic quotient of 1.0.

We analyzed biomass and nutrient content of attached algae along depth gradients in 2011 and 2013. In 2011, divers collected 3 replicate epilithic periphyton scrubs from large boulders or bedrock from 0.5, 1, 2, 3, 4, 5, 6, 7, and 8 m using a 1 cm diameter modified syringe sampler with a wire brush (Loeb, 1981). Two replicates from each depth were acidified by adding hydrochloric acid (1 N-HCl) one drop at a time until the sample stopped emitting CO_2 gas. This step was necessary to remove inorganic C (carbonate) before P (phosphorus) analysis. One replicate from each depth was frozen without acidification for subsequent chlorophyll-*a* analysis.

In 2013, divers collected cobbles (N=4 per depth) from 1, 2.5, 5 and 7 m in order to obtain a larger mass of periphyton to measure chlorophyll a, Ash Free Dry Mass (AFDM), fatty acid content, and C:N:P. Cobbles were scrubbed within 1 hr of collection by placing a 25.5 cm^2 plastic cap over a uniform portion of the upward facing side of the cobble. Periphyton outside the cap was removed with a wire brush and retained for ash free dry mass (AFDM) analysis. After removing the periphyton outside the cap, the quantitative periphyton sample was scrubbed from the rock surface, collected and centrifuged. The pellet was frozen in pre-weighed glass vials and then freeze-dried (Virtis, Gardiner, NY) for subsequent analysis of chlorophyll-*a,* fatty acids and C:N:P.

Periphyton P content was analyzed using the acid molybdate method for particulate samples (APHA, 1995). Duplicate subsamples (~ 5 mg) were combusted for 1 hour at 500 °C and then digested in acid for 2 hours at 102 °C. Absorbance was read at 880 nm on a micro plate reader (Bio-Tek Instruments, Winooski, Vt). Periphyton C and N content were analyzed at Cornell stable isotope laboratory with a Vario EL *I II* elemental analyzer (Elemental Americas, corporation, NJ, USA). Chlorophyll-*a* was analyzed by extracting subsamples in 90% buffered ethanol at 4 ^{0}C for 24 hours and measuring fluorescence on a Turner Aquafluor fluorometer (2002). The proportion of organic matter (AFDM) in periphyton was obtained after combustion in a muffle furnace for 4 hours at 550 °C (APHA, 1995).

Total lipids were extracted from ~ 0.3 g of a lyophilized subsample using a ratio of 2:1 methanol: chloroform mixture (DeForest et al., 2012). I used the standard

phospholipid 19:0 to determine lipid recovery. The phospholipid-derived fatty acids (PLFA) fraction was separated from total extracted lipids using silicic acid solid-phase extraction chromatography columns (500mg 6 ml^{-1}). The extracted phospholipids were converted to fatty acids methyl esters (FAMEs) and separated using a HP6890 GC-FID gas chromatograph (Agilent Technologies Inc., Santa Clara, California, USA). We identified individual PLFA using the Sherlock® Microbial Identification System (MIS) (MIDI, Inc., Newark, Delaware, USA). Response values generated from the Sherlock MIS were converted to a percent mole fraction of total PLFA.

Statistical analyses: Unless otherwise stated, all analyses were performed using R software (R Development Core Team 2012). For the 2011 data, I used linear mixed effects analysis to test the effects of depth and sites on fish density (log(x+1) (lmer4 ; Bates 2012). I used the same approach to test for the effects of depth and site on habitat complexity (rugosity), periphyton phosphorus (%), and chlorophyll- *a,* with depth as a fixed factor and site as a random factor. Each analysis was done independently.

I used mixed models to assess the effects of depth on periphyton quality and quantity on the 2013 algal scrubs (Bates, 2012). Metrics of algal quality included essential fatty acid (percent mole fraction - EFA), % N, % P, % C, molar ratios of C:N, C:P and N:P and quantity metrics included chlorophyll-*a* (mg/m^2), sediments (g/ m^2), phosphorus (g/m^2) and carbon (g/m^2). I entered depth as a fixed factor and site a random effect. Each analysis was done separately. Model selection was based on the significant

p-values obtained by likelihood ratio tests of the full model against the reduced model. When the effect of site was significant, Tukey's HSD method was used to compare between sites. I also calculated average C:P and N:P at each depth and site to compare them to periphyton nutrient ratios under optimal nutrient conditions (Hillebrand and Sommer, 1999). Comparisons with optimum values were made using one sample t-tests.

After testing changes in algal quantity and quality as a function of depth, I reduced the 2013 algal data set by removing the data from 5 and 7 m because algivore densities declined markedly below 3 m. First, I calculated a mean value for each parameter for the two remaining depths (1 and 2.5 m) and then calculated a mean for each site. I used principal components analysis (PCA) to identify minimum sets of periphyton diet predictors which were more likely to explain the differences in fish distribution and condition factor among sites. Several diet parameters were correlated. Therefore, I used correlation and pricomp function in R to conduct our PC analysis. The first two components accounted for 96 % of the variance (Fig.3.1). The PC1 axis had highest loading for metrics related to algal quantity including C (g/m^2), organic matter (g/m^2) and inorganic sediment (g/m^2) and the PC2 axis had the highest loadings for metrics of periphyton quality including % P and chlorophyll a concentration (mg/g). Percent N and % P were highly correlated (r=0.96) and we chose to use %P as a predictor variable due to the high demand that fish have relative to N (Ye et al., 2006).

I used 2013 data to regress *T. brichardi* densities and on periphyton % P and periphyton chlorophyll concentration (mg Chl/g biofilm) to quantify the effects of among

site variation in food quality on algivore density and condition factor. I performed regression to assess the effect of EFAs on fish density. I used stepwise elimination of insignificant value and lower *Akaike Information Criterion* (*AIC*) to select the model. We performed similar analyses using average condition factor at each site as the response variable. I also used Pearson's product correlation to test for relationships between fish densities, inorganic sediments and condition factor. I tested for effects of among site differences in piscivore densities and habitat complexity on *T. brichardi* densities using general linear model. I used Tukey's HSD tests to determine which site differed when significance was observed.

3.4 Results

Overview of fish distributions among sites: We counted a total of 814 *Tropheus brichardi* and 336 *Petrochromis kazumbe* in the algivore surveys in 2011 and 616 *T. brichardi* in 2013. *Tropheus brichardi* densities were weakly correlated between 2011 and 2013 (Pearson's correlation = 0.49, p = 0.121), except that sites 3 and site 13 which had the highest densities in both years Condition factor varied significantly among sites and declined over the 3 years study period. The mean condition factor for *T. brichardi* was 3.83$\pm$ 0.06 , 2.67 $\pm$ 0.03 and 2.10 $\pm$ 0.07 (mean $\pm$ SE) in 2011, 2012 and 2013 respectively. There was no relationship between condition factor and fish density at a given site in either 2011 or 2013 (Pearson's cor. 0.3, $p = 0.5$). Algivores densities were nearly 3 times higher than piscivores densities, and there was no relationship between algivore densities at a site and piscivore densities ($P > 0.05$). If we removed site 2 from the analysis, there was a positive relationship between the density of algivores and piscivores among sites ($f_{1,9} = 6.69$, $P = 0.029$; Fig.3.4). Among-site variation in habitat complexity did not explain variation in algivore densities ($P > 0.05$).

Overview of among site variation in algal composition. Principal component analysis (PCA Fig. 3.1) revealed that the first two components accounted for 71.5 % of the variance (Fig.3.1). The PC1-axis had highest loading for sediments (g/m^2) and organic matter (g/m^2) which are indicative of food quantity and the PC2-axis had the highest loadings for Chl-a (mg/g), % P which indicates food quality.

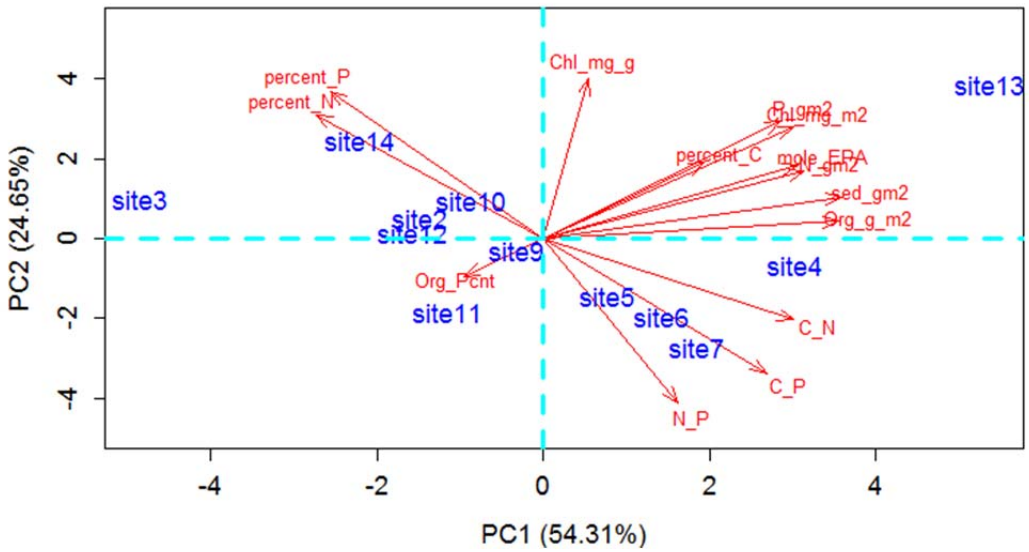

Figure 3. 1: The PCA results for periphyton quality and quantity at each site, data collected from Lake Tanganyika, in 2013. PC1 represents food quantity g/m^2 (organic matter and sediment) which increases from left to the right and PC2 represents food quality (% P and chl a in mg/g) which increases from bottom to the top. Dashed line separates between high and low food values.

Effects of depth on the within-site distribution of algivores and their food: We used the 2011 data to assess the relationship between fish density and depth. The density of *T.brichardi* and *P.kazumbe* declined with depth ($p < 0.05$). Depth accounted for 60 % of the variation in algivore density within sites ($p < 0.05$). *Tropheus brichardii* had significantly higher densities at sites 3 and 13, whereas the heavily sedimented site 7 had the lowest densities (along depth gradient, $p < 0.05$). *Petrochromis* kazumbe at site 2, 4, and 12 were significantly higher than at other sites (Tukey's HSD tests, $p < 0.05$)

The data from both 2011 and 2013 demonstrate a significant decline in periphyton quality with depth whether quality was measured as nutrient content, chlorophyll a concentration (µg/g) % P or EFA concentration (Fig.3.2 b and c, Table 3.4). Percent carbon did not change with depth ($p > 0.05$, Table 3.4), but periphyton N: P and C: P ratios increased significantly with depth ($p < 0.05$, Table 3.4). The N: P ranged from 14 to 17 at 1 and 7 m, respectively and C: P ranged from 83 to 727. The average C: P at 1 m was 251± 21, and at 7 m was 363 ± 22 (mean ± standard error). Both values were significantly higher (One tailed T test, $P < 0.05$) than the optimal value of C: P for periphyton (106-180; Kahlert et al., 2002, Hillebrand et al., 2004)

In 2011, chlorophyll-a content of periphyton increased significantly with depth ($p = 0.012$; Fig. 3.2c; Table 3.2) ranging from 14 µg/mg ± 4.1 at 1 m to 23 µg/mg ± 3.6 (mean ± se) at 8 m depth. In 2013, we found a negative relationship between chlorophyll concentration and depth (Table 3.2).

Table 3. 2: Mixed regression model to explain the effects of depth on fish density (*T. brichardi* and *P. kazumbe*), habitat index, phosphorus (%) and chlorophyll- α. Data collected between June and August, 2011.Each parameter was analyzed separately.

Parameters	estimate ± SE	X^2	df	P value
T. brichardi	- 0.313 ± 0.01	132.7	3	< **0.05**
P. kazumbe	- 0.186 ± 0.01	220.3	3	< **0.05**
Habitat- index	- 0.01 ± 0.01	4.161	3	0.344
Phosphorus (%)	- 0.007 ± 0.0	13.93	3	**0.002**
Chlorophyll-α (mg/g)	0.105 ± 0.05	10.81	3	**0.012**

Notes: Mix liner model with p -value showing the most parsimonious predictors. Data collected at water depth 0.5, 1, 2, 3, 4, 5, 6, 7 and 8 (N = 9). In a model, depth was included as a fixed variable and site as a random variable. Significant effects are marked in boldface type, with positive value of estimate indicating a positive slope and vice versa. Fish density was log transformed (x+1).

Polyunsaturated fatty acids (PUFA) decreased significantly with depth, whereas Monosaturated fatty acids (MUFA) and saturated fatty acids (SAFA) increased with depth (Table 3.4). The most abundance Essential Fatty acids (EFAs) were Eicosapentanoic acid (EPA) and Linoleic acid (LA) which constituted 1.5% and 3.2% respectively of the total fatty acids.

I did not analyze periphyton quantity from 2011 due to small sample size. However in 2013, metrics of periphyton quantity (mass/m^2) decreased significantly with depth, including C, N, P, chlorophyll a and sediments (Table 3.4). Depth had no effect on the quantity of periphyton organic carbon ($F_{1,114} = 0.017$, $p > 0.9$), AFDW (g/m^2; $F_{1,114} = 1.8$, $p > 0.14$), or N ($F_{1,114} = 0.6$, $p > 0.43$). Periphyton productivity measured as PAM fluorescence declined with depth at all sites except site 7 (Fig. 3.1d).

Based on the 2011 depth transects densities of *T. brichardi* and *P. kazumbe* were both positively related to periphyton P content within sites ($p < 0.05$, Table 3.3). The relationship between fish density (for *T.brichardi* and *P. kazumbe*) and chlorophyll a (μg/g) was negative but not significant ($p > 0.05$).

Habitat complexity was not a linear function of depth. Rather the habitat index tended to reach a maximum at about 3 m (Fig. 3.1a). Thus, between 0.5 and 3 m, where fish were most abundant, there was a slightly negative relationship between fish density and habitat index (Fig.3.2a). The habitat index at site 7 was significantly lower than at other sites (ANOVA $p < 0.05$)

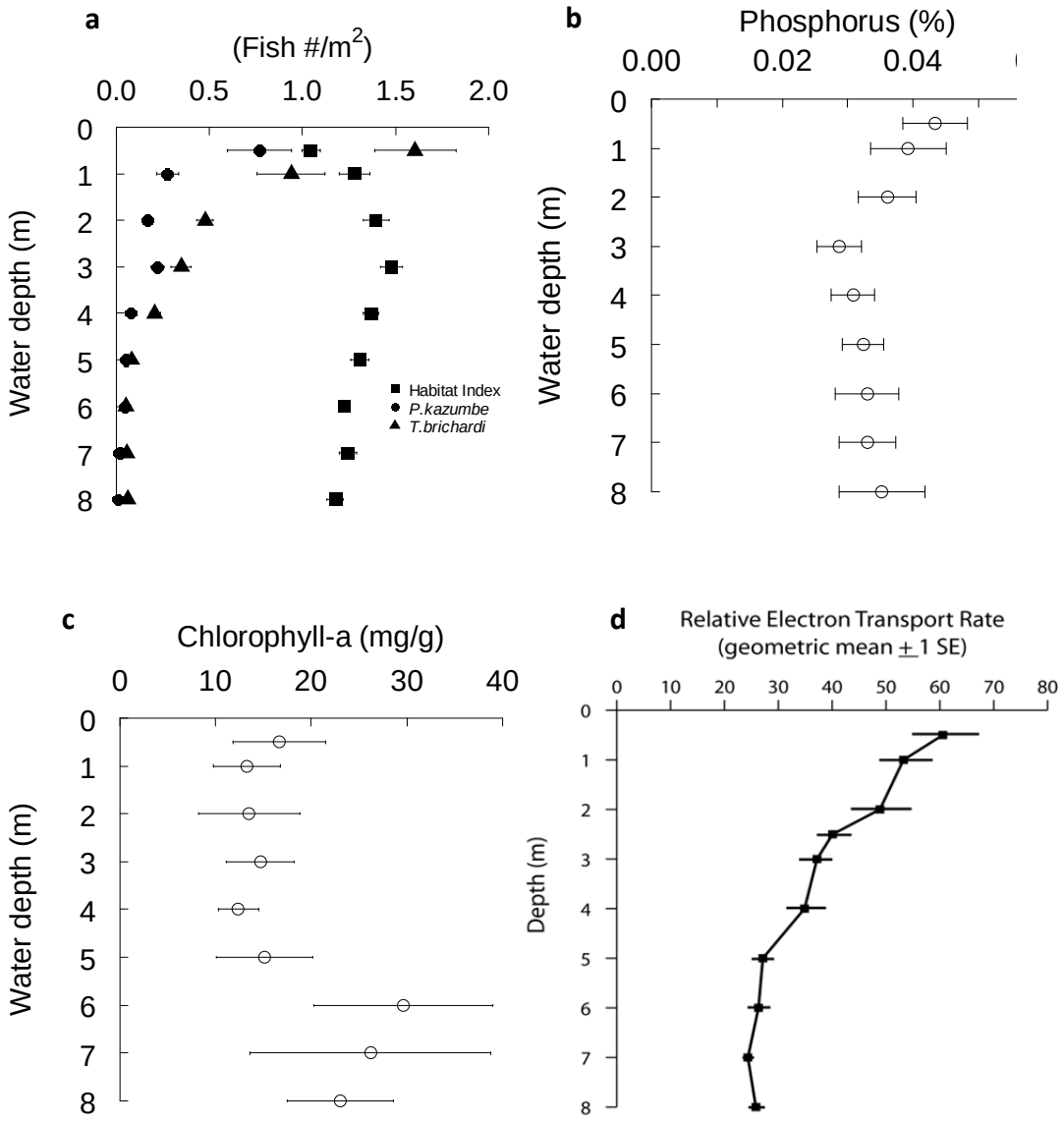

Figure 3. 2: Depth profiles of (a) fish density (*Tropheus brichardi* and *Petrochromis kazumbe*) and habitat index (b) phosphorus (%) (c) chlorophyll-α (mg/g) in Lake Tanganyika, data collected from June to August, 2011 and 2013. Each point represents the average fish density across sites at each 1 m depth interval. The error bars represents the standard error of the mean.

Among-site variation in algivores and periphyton (2013): We used multiple regressions to determine either quality or quantity could account for the variance in fish abundance among sites. Among-site variation in *T. brichardi* was positively correlated with periphyton quality, negatively correlated with periphyton standing crop (excluding site 13 which was an outlier) and uncorrelated with periphyton gross primary productivity. *Tropheus brichardi* densities was positively correlated with periphyton % N (Fig. 3.3a; $F_{(1,10)} = 5.43$; $p < 0.011$) and % P (Fig. 3.3b; $F_{(1,10)} = 6.66$, $p = 0.03$) and. there was a largely negative, but not significant, correlation between *T. brichardi* densities and N: P (Fig. 3.3e; $p < 0.10$) and a significant negative correlation between fish densities and C:P (Fig. 3.3f; $p < 0.034$). Algivore densities were not correlated with periphyton chlorophyll content (mg/g) (Fig.3.3c; $F_{(1,10)} = 0.45$; p = 0.49), and among-site variation in condition factor was positively but not significantly correlated with chlorophyll content of periphyton ($p > 0.05$).

Among-site variation in periphyton standing crop was negatively correlated with fish densities. The total amount of periphyton N, C, and chlorophyll per square meter of rock surface declined as a function of algivore density (Fig. 3. 4), but the relationship with P (g/m^2) was not significant (Fig. 3.4b; $p < 0.1$)

Unsaturated fatty acids (% mole of EFA, PUFA and LIN) were negatively related to % P ($p < 0.05$) whereas, ARA, EPA (20:5w3) and DHA (20:6w3) did not change with % P ($p > 0\ 05$). We found no significant correlation between EFAs as the single variable and fish density ($p > 0.05$), but the effect of the essential fatty acid on the

density appears to occur only in conjunction with % P (Table 3.5). The final equation with the combination of both % P and EFAs is :

Fish density = -0.15 + 1.93 (% phosphorus) + 0.02(% mole-EFA) + error.

The amount of inorganic sediments coating the rocks varied significantly among sites (regression, $p < 0.05$). Sites 4, 6, 7 and 13 had higher inorganic sediments deposition than other sites (Tukey's HSD tests). There was a significant negative relationship between sediment on rocks (g/m^2) and fish density ($p < 0.05$; Fig. 3.4e). Site 13 was excluded because it was an outlier.

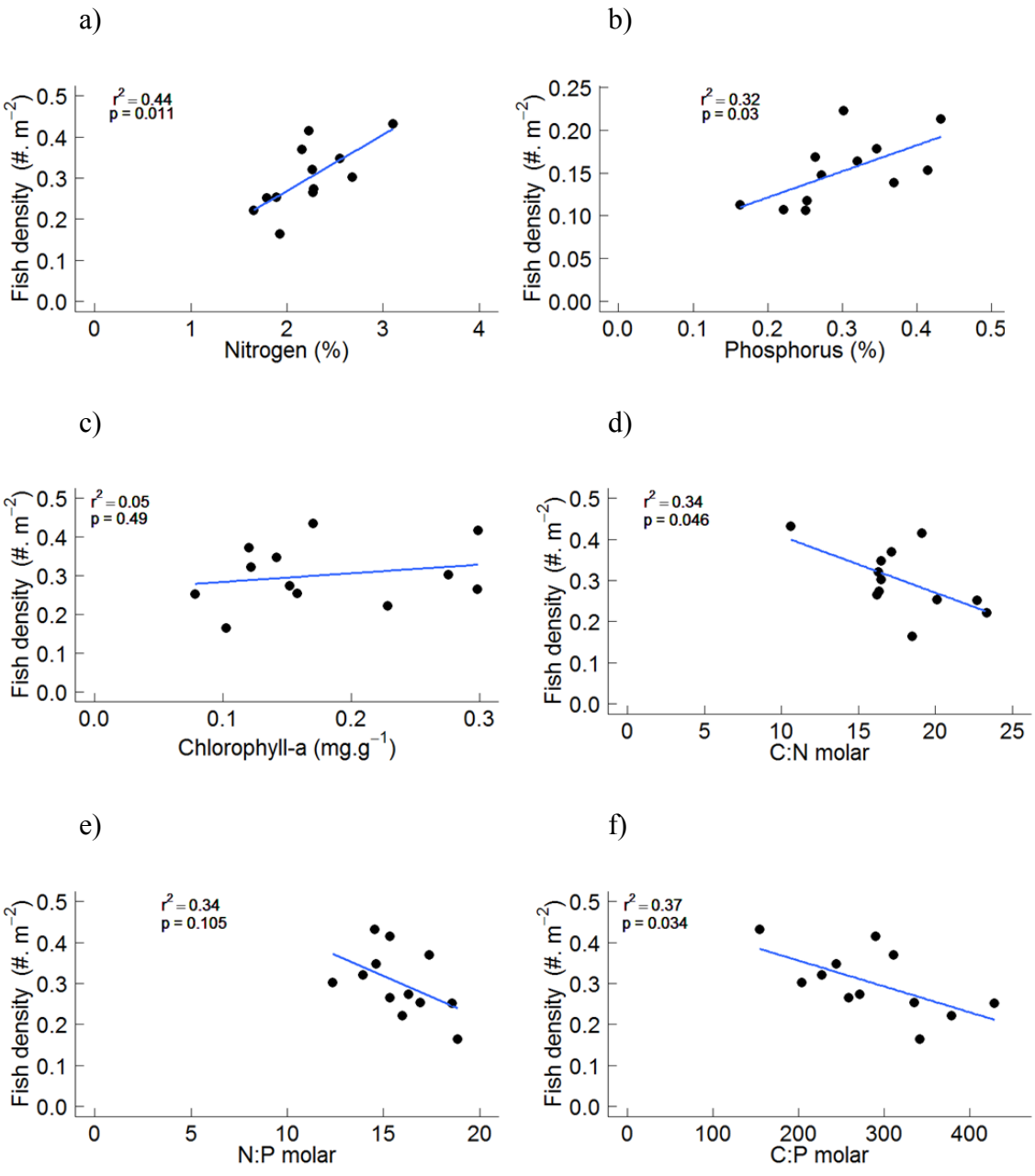

Figure 3.3: Mean fish density (#/m2) in relation to periphyton quality (a) nitrogen %, (b) phosphorus %, (c) chlorophyll (d) C:N molar (e) N:P molar (f) C:P molar. Data collected from June to August, 2013. Values plotted are means at 1 and 2.5 m depth pooled within site fitted with regression line.

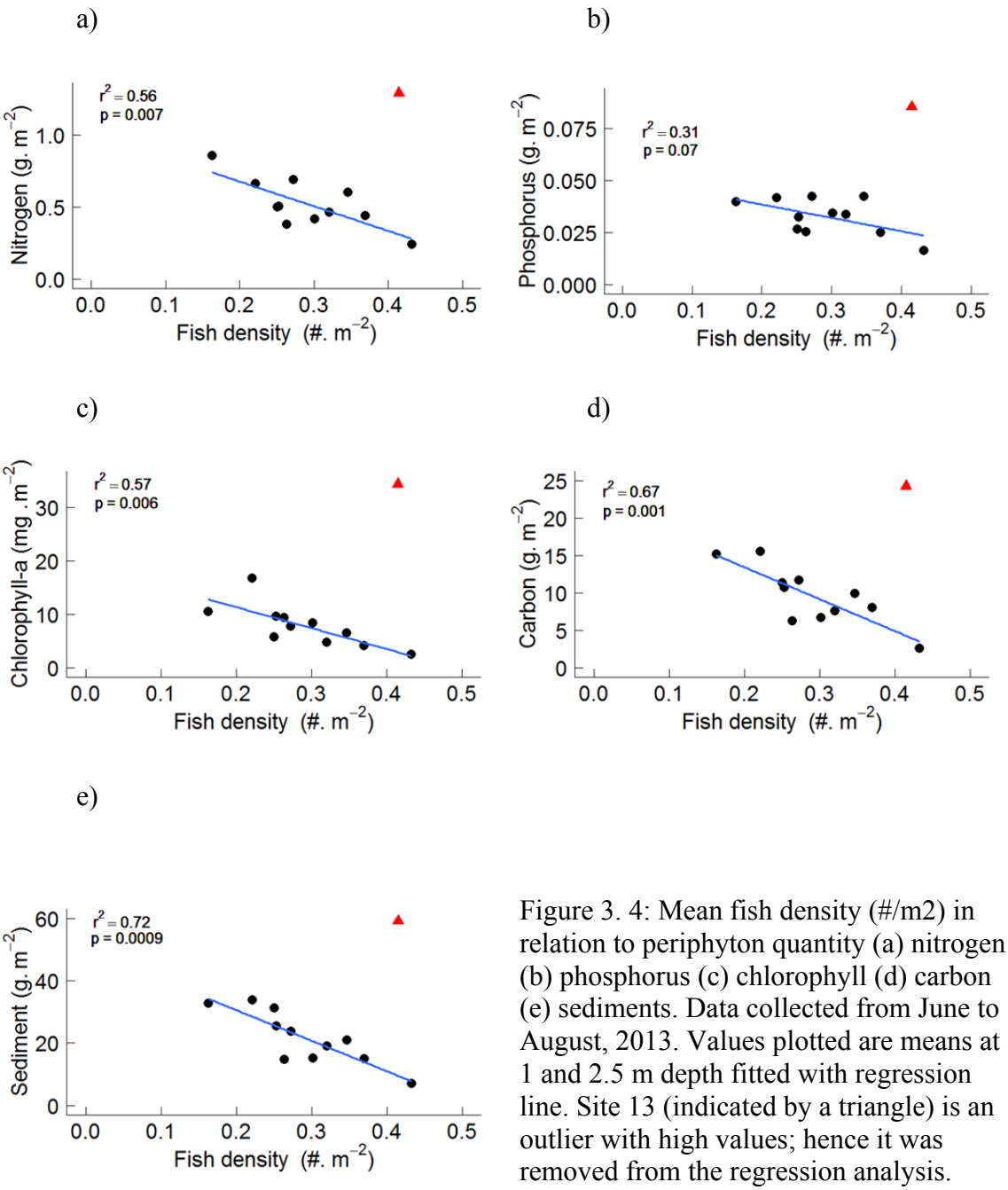

Figure 3. 4: Mean fish density (#/m2) in relation to periphyton quantity (a) nitrogen (b) phosphorus (c) chlorophyll (d) carbon (e) sediments. Data collected from June to August, 2013. Values plotted are means at 1 and 2.5 m depth fitted with regression line. Site 13 (indicated by a triangle) is an outlier with high values; hence it was removed from the regression analysis.

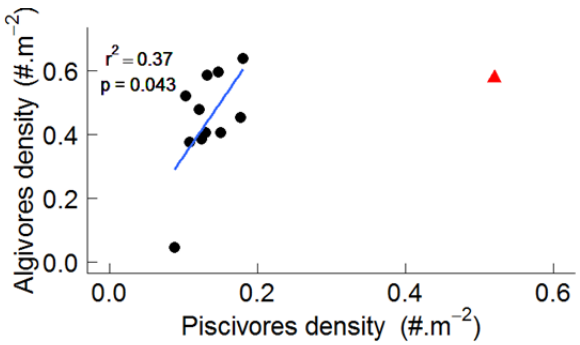

Figure 3.5: Regression result of algivorous fish density as a function of piscivores, fitted with regression line. Data collected from 2009 to 2013 at 1 to 5 m (McIntyre et al., Unpublished). Site 13 (indicated by a triangle) is an outlier with high values; hence it was removed from the regression analysis.

Table 3. 3: Linear regression for the relationship between fish density (a) *T. brichardi*, (b) *P. kazumbe*, in relation to periphyton % phosphorus, habitat index and chlorophyll-a across 12 sites. Data collected at 0.5 to 3 m depth, between June and August, 2011.

Parameter	Estimate	SS	MS	DF	F-value	P-value
a) Log-*T.brichardi* with						
Periphyton (% phosphorus)	10.226	0.394	0.394	1	20.582	**0.036**
Log-habitat-index	-0.681	0.523	0.523	1	7.995	**0.017**
Log-chlorophyll-a	-0.0225	0.014	0.014	1	2.448	0.68
Error		2.284	0.081	28		
b) Log-*P. kazumbe* with						
Periphyton (% phosphorus)	3.251	0.087	0.087	1	2.235	0.146
Log-habitat-index	-0.195	0.051	0.051	1	1.303	0.263
Log-chlorophyll-a	-0.047	0.063	0.063	1	1.622	0.213
Error		1.098	0.039	28		

Notes: Liner model with p -value showing the most parsimonious predictors. Significant effects are marked in boldface type, with positive value of estimate indicating a positive slope and vice versa. Fish density, habitat index and chlorophyll were log transformed. DF, degrees of freedom; SS, sum of squares; MS, mean squares.

Table 3. 4: Linear regression models for periphyton food (quality and quantity) as a function of depth for the 12 sites, data collected between June and August, 2013. Each parameter was analyzed independently. Significant effects are marked in boldface type.

Response variable	Slope ± SE	F value	P value
Quality - stoichiometry			
Log-Phosphorus (%)	- 0.005 ± 0.001	(1,125) 28.65	< **0.05**
Carbon (%)	- 0.12 ± 0.1	(1,125) 18.24	0.22
Nitrogen (%)	- 0.04 ± 0.01	(1,125) 11.31	< **0.05**
Log-Chl.a (mg/g)	- 0.11 ± 0.03	(1,125) 8.41	**0.004**
C:N molar	0.64 ± 0.02	(1,125) 10.08	**0.001**
C:P molar	19.19 ± 40	(1,125) 17.44	< **0.05**
N:P molar	0.53 ± 0.17	(1,125) 8.33	**0.004**
Quality-fatty acid			
SAFA (%mole)	1.79±0.8	(1,45) 4.6	**0.03**
MUFA (% mole)	0.89±0.5	(1,45) 2.7	0.108
PUFA (%mole)	-0.74±0.2	(1,45) 8.7	**0.004**
DHA+EPA (%mole)	-0.21± 0.08	(1,45) 6.1	**0.017**
DHA(%mole)	-015 ±0.005	(1,45) 6.6	**0.013**
EPA (%mole)	-0.012 ± 0.02	(1,45) 5.8	**0.018**
LI (%mole)	-0.18±0.08	(1,45) 4.5	**0.037**
AA (%mole)	-0.052±0.02	(1,45) 2.6	**0.011**
Quantity			
Carbon (g/m2)	- 0.22 ± 0.02	(1,125) 0.73	0.36
Nitrogen (g/m2)	- 0.02 ± 0.01	(1,125) 3.65	0.05
Phosphorus (g/m2)	-0.002 ± 0.00	(1,125)12.66	< **0.05**
Sediment (g/m2)	- 0.08 ± 0.06	(1,125) 0.02	0.87
Org. matter (g/m2)	-0.6 ± 0.07	(1,125) 0.76	0.38
Chlorophyll-a (mg/m2)	- 0.84 ± 0.30	(1,125) 6.72	**0.011**

Notes: Periphyton sample were collected at 1, 2.5, 5 and 7 m (N= 3 per depth), intercept, slope, f-value and p-values are provided. DF, degrees of freedom; SS, sum of squares; MS, mean squares.

Table 3. 5: Summary table of the analysis of variance between fish density with EPA (% mole), and P (%), data collected 2013. Significant effects are marked in boldface type.

Response: Density (#/m^2)						
	Slope	Df	SS	MS	F value	P value
Phosphorus (%)	1.815	1	0.027	0.026	10.022	**0.011** *
EPA (% mole)	0.043	1	0.019	0.019	7.146	**0.025** *
Error		9	0.024	0.002		

DF, degrees of freedom; SS, sum of squares; MS, mean squares.

3.5 Discussion

Variation in algivore densities among isolated habitats were not related to habitat structure or predator density. Rather, algivore densities were positively correlated with algal quality both within and among habitats. The quantity of algal resources available to algivores declined as a function of depth within sites even though the strongest grazing pressure, inferred from algivore densities, likely occurred at the shallowest depth. Among sites, periphyton quantity was negatively correlated with fish density. The negative among-site relationship between fish density and periphyton organic carbon and chlorophyll (g/m^2) indicates a strong top-down effect of fish on periphyton biomass. The within and among-site positive correlation between algivore densities and food quality is consistent with a metabolic cost to consuming low quality food (either from high C:P or from ingestion of sediment). This cost appears to yield lower densities of herbivores at sites with high sediments.

Distribution of fish within sites in relation to food quality and quantity: Within sites, fish aggregated in shallow areas where food availability was highest. Periphtyon biomass (Table 3.4) and productivity (Fig. 3.1) declined with depth, though the rate of decline varied among sites ($p < 0.05$). Photosynthesis measured as relative electron transport rate (rETR) declined with depth between 0.5 and 8 m at all sites except site 7, which had the highest accumulation of sediments. Primary production measured as oxygen exchange was significantly higher at 2.5 m than at 5 m at most sites. Light is an overriding

determinant of algal biomass and productivity in lakes throughout the world (Karlsson et al., 2009; Vadeboncoeur et al., 2008, 2014) and the negative relationships between both productivity and biomass with depth are consistent with light limitation of periphyton in the littoral zone of Lake Tanganyika. Increases in the territory size of algivorous cichlids in Lake Tanganyika as a function of depth have been attributed to declines in algal productivity with depth (Sturmbauer et al., 2008; Karino et al., 1998), but our data are the first to document both declines in algivore densities and declines in algal productivity. The concentration of algivores in the shallow areas in each site corresponds with maximal algal food availability (food quantity) and is similar patterns in streams where fish closely track resource availability (Power, 1984)

Within sites, fish densities were also positively correlated with food quality because the concentration of N, P, and EFA's was highest at depths < 3 m. We had expected algal quality to decrease with depth based on the light-nutrient (Sterner et al., 1997). The light-nutrient hypothesis was developed for phytoplankton and predicts an increase in algal C:P ratios with declining light availability in the water column due to declining rates of photosynthesis (C uptake). An unstated assumption of this hypothesis is that nutrient availability and uptake is either invariant with depth or varies less than carbon fixation. The increase in C:N and C:P with depth suggests that both nutrient availability and light declined with depth at our study sites, and that the nutrient availability gradient was more pronounced than that of light. Fish constitute a significant flux of nutrients through excretion (Andre et al., 2003; McIntyre et al., 2008) and fish

excretory products can provide a substantial portion of the nutrients necessary for algal growth (McIntyre et al., 2006; Schindler and Eby, 1997; Schindler et al., 1993; Zimmer et al., 2006). Thus, the decline in algivores themselves may contribute to a decrease in nutrient availability with depth, and hence an increase in algal C:P and C:N. The increase in C: P ratio with depth suggests increasing P limitation for algal growth with depth because the values exceed the range of optimal ratios 106-258 (Hecky and Kilham, 1988, Hecky et al., 1993; Hillebrand and Sommer, 1999). This interpretation assumes that other trophic guilds that occur deeper do not recycle nutrients as a rate similar to the algivores. Regardless of the mechanism underlying the depth gradients in periphyton productivity and quality, the concentration of algivorous fish in shallow areas allows them to maximize energy intake (Napp et al., 1988) and nutrient acquisition.

Periphyton appears to be colimited by N, P, and light, but the fish that rely on attached algae appear to be very sensitive to P availability. Inorganic nitrogen and phosphorus are below detection limits at all sites during all seasons (McIntyre, unpublished data), making it difficult to assess N versus P limitation of periphyton based on water concentrations. The attached algae community biomass is dominated by N-fixing cyanobacteria and diatoms, many of which also fix N (Bohme 1998; Golden and Yoon, 2003). The dominant source of new P to the epiliminion of the lake is periodic upwelling events (O'Reilly et al., 2003; Kilham and Kilham, 1990; Alin and Cohen, 2003). The N:P ratio of periphyton (mean= 15.8± 0.7) is close to optimal values (16 -18, Kahlert, 1998; Hecky et al., 1993; Hillebrand and Sommer, 1999). Thus, periphyton

growth in Lake Tanganyika is probably colimited by both N and P (Jarvinen et al., 1999; McIntyre et al., 2006). Periphyton N and P content declined with depth, but the change in P was more marked, and N:P ratios increased with depth indicating increasing P limitation of algae (Table). The average N: P ratio of 15.8 in periphyton was 6 times higher than the N: P ratio in *T.brichardi* tissue (2.5) (McIntyre unpublished data). This mismatch in elemental status between the fish and its diet suggests that fish have will have a greater difficulty in meeting their P needs relative to N. Fish have a high P demand because P is required for bones, teeth (Sterner and Elser, 2002) and scales (Ohira et al., 2007)

Periphyton quality measured as essential fatty acids also decreased with depth, and these essential fatty acids are critical for the growth and development of fish. The changes in EFA with depth may reflect turnover of microbial taxa with depth in response to gradients in light and nutrients (Hill et al., 1995, Sterner et al., 1997). The lipid content of algal communities reflects taxonomic composition (Gatenby et al., 2003; Bigogno et al., 2002; Volkman et al., 1989). Diatoms and cyanobacteria dominate the Lake Tanganyika periphyton community with small contributions of chlorophytes, or green algae. Diatoms are rich in EPA and DHA, whereas cyanobacteria and other bacteria do not produce long chain essential fatty acids. The decline in EFA with depth and their replacement with increasing contributions of SAFA and MUFA suggests decreasing contributions of diatoms and increasing contributions of bacteria to the periphyton community as a function of depth. It is notable that these changes are detectable within

the first 5 m of the 60 m euphotic zone of the lake. The highest quality algae in terms of both P content and fatty acid content occur at very shallow depths (< 5 m) which correspond to the highest densities of algivorous fish (Fig 3.1b, Table 3.4).

Tropheus brichardi could select areas within sites that either maximized energy gain or minimized predation risk. We did not measure predation risk as a function of depth. It is theoretically possible that algivores aggregated in the very shallow areas to avoid predation, but it is not obvious how the shallow environment would provide a predation refuge from piscivores, and the proximity to shore almost certainly increased predation risk from avian predators such as kingfishers (Power, 1992). Furthermore, behavioral observations demonstrated that *T. brichardi* spent the majority of time actively foraging (swimming and feeding) and a very small percentage of time engaging in hiding or agonistic behaviors that might correspond to avoiding predation (Chapter 2). Thus, our data offer compelling evidence that *T. brichardi* distributions within habitats are determined by resources, including both the rate of food supply (algal productivity) and the nutrient content of the resource (algal quality).

Among-site variation in T. brichardi densities in relation to food quality and quantity: Variation in algal productivity and quality within sites is highly correlated with depth (light) gradients and algivores can easily swim to areas of highest food availability. However, each of our individual sites was surrounded by expanses of sand which rock dwelling species are reluctant to cross the sand. Thus, each rocky site can be viewed as an

isolated population with densities that reflect resource availability (both food and habitat) and predation pressure. Predators affect the choice of habitat of algivores in streams and on coral reefs (Power et al., 1985). This can lead to high densities of herbivores in areas with low predation pressure (Gilliam and Fraser 2001). Our results suggest that variation in algivore densities among sites was not due to predation. Densities of algivores were nearly 3 times higher than piscivores densities (predators) and the relationship between the two was positive or neutral (Fig.4). Rather, *T. brichardi* densities in Lake Tanganyika were correlated with periphyton quality.

If digestive and metabolic costs are lower with a higher quality diet, this will translate to higher energy gain per gram food, and hence higher growth per unit of carbon ingested (chapter 1). Growth is tied to protein availability as well as the energy to convert protein into growth. High food quality may enable individual fish to allocate and store excess energy for future demand such as reproduction, predator avoidance or period of low food availability (Green and McCormick, 1999). The best single predictor of the distribution of *T. brichardi* appeared to be % P, as it was found earlier for Daphnia (Urabe et al., 1997). Our result indicates that the effect of the essential fatty acid (EFAs) on fish density appears to occur only in conjunction with % P (Table 3.5). Thus, the effect of EFAs on the density was probably synergetic. In our study, periphyton % P and EFAs were very negatively correlated ($p = 0.04$). This relationship most likely was caused by sediments. *Tropheus* feeds selectively on high diatoms (Chapter 2). Hence the

negative relationship between fish density and EFAs among sites may be due to low grazing pressure in sediment sites.

There is strong evidence that the phosphorus content of herbivore diets affects growth rates, but this is rarely studied in the context of herbivore densities in natural ecosystems. The growth rate hypothesis (GRH) proposes that consumers with high growth rate will have relatively high P concentration in their tissues because high growth rates requires high P allocation into ribosomal RNA in order to supports protein synthesis (Sterner and Elser, 2002). High growth rates may facilitate reproduction success by allowing organisms to reach reproductive maturity at a younger age, thus producing more generations in a given time (Sterner 1993, Frost et al., 2004, Diekmann et al., 2009). All of these factors can contribute to faster growing and better conditioned fish when food quality is high, but our results indicate that high quality algae leads to a reduction in the amount of primary production necessary to support an individual fish. Others have demonstrated that algivores in Lake Tanganyika need larger territories in deeper areas in order to compensate for lower rates of primary production (Karino 1998, Sturmbauer 2008). Our data show that they also need larger territories when the nutrient content of their food is low.

Among sites, *T. brichardi* density is negatively correlated with food quantity. A possible mechanism for the inverse relationship between food quantity and food quality among sites is that sediments impose a metabolic cost that leads to lower densities of algivores. Where there are lots of fish, accumulation of periphyton biomass is low. This

indicated a top-down control of algal biomass. Herbivorous act as agents of top-down control and their grazing on periphyton reduces the abundance, diversity and productivity of photosynthetic organisms (Steinman, 1996; Rosemond and Mulholland, 1993; Hillebrand and Kahlert, 2000; Burkpile and Hay, 2009). In addition, grazers affect the taxonomic composition of periphyton. Algivorous fish feed selectively on palatable and nutritious diatoms (Chapter 2, and Anderson et al., 2009). Periphyton standing crop was inversely related to fish densities, and low consumption of algae may be the mechanism behind the higher concentrations of EFAs at sites with relatively low algivore densities (PCA Fig. 3.2**)**. We have conducted field experiments that demonstrate that when algae are protected from grazing, biomass and productivity rapidly increases (Vadeboncoeur and McIntyre, unpublished data).

In Lake Tanganyika, agriculture activities and construction along the lake shore have increased the amount of sediments deposition. The negative relationship between fish density and sediment accumulation (Fig.1.5) may be due to the negative effects of sediments on digestion. Our behavioral data show that *T. duboisi* feed more slowly in heavily sedimented sites, suggestion that they may be trying to avoid ingesting sediments. Ingested sediment may slow the growth and reproduction of algivorous fish (Newcombe and Macdonald, 1991) and ultimately result in population reductions (Henley et al., 2000). We thought that sediment deposition might have a negative effect on primary productivity by reducing light penetration (Van Nieuwen huyse and LaPer riere, 1986), but our results do not support this. Suspended sediment also may cause respiratory

problems in fish by clogging their gills (Bruton, 1985), dilute algae and lower the relative abundance and nutritional value of algae (Gilbert et al., 2005, McIntyre et al., 2005; Yamada and Nakamura 2002). Poor nutritional values have shown to decrease also fecundity of zooplankton and survivorship (Kilham et al., 1997), this possible could be one of the reasons for low fish density in sediments sites. We found strong positive correlation between sediments and organic matter, where there are a lot of sediments, algal biomass is high, due to low fish density. This may be due to the strong negative effect of sediments on fish grazing pressure. Sediment reduces the strength of top down control.

Appendix A

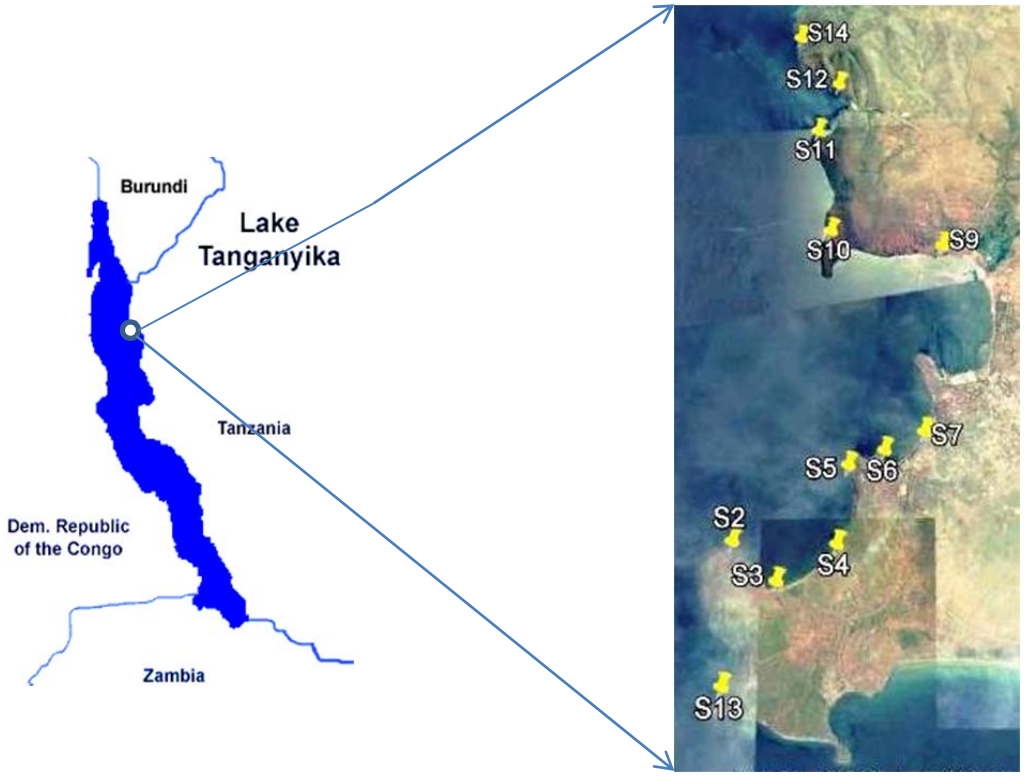

Figure A1: Lake Tanganyika study sites.

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