

Nutrient recycling by *Tropheus brichardi* across a littoral productivity gradient in Lake Tanganyika

Student: Tana Hintz

Mentor: Peter McIntyre

Introduction

Nutrient recycling occurs when nutrients are released into the environment by animals or microbial consumers. Fish-mediated nutrient recycling is an important source of nutrients for primary producers in many aquatic ecosystems, sometimes even exceeding external loading rates (Attayde and Hansson 2001). Consumers release non-assimilated nutrients as liquid waste that is available to primary producers or as feces that is available after further degradation. Most studies on recycling have focused on nitrogen (N) and phosphorus (P) because these elements often limit primary production (Vanni 2002). N and P concentrations in the surface waters of Lake Tanganyika are low, and nutrient supplementation enhances algal growth rates (Thoms this volume).

The study of ecological stoichiometry addresses the balance between cycles of many elements in ecosystems. Among its basic principles is that animals maintain homeostasis in body nutrient composition and consequently, the rates at which they recycle nutrients reflects the imbalance between their bodies and food resources (Sterner and Elser 2002). However, few studies have examined nutrient recycling rates by a single consumer species across a gradient of food stoichiometry.

The purpose of my study is to determine the variability in NH_4 and soluble reactive phosphorus (SRP) excretion by an herbivorous cichlid fish (*Tropheus brichardi*) across a littoral productivity gradient in Lake Tanganyika. A previous study of *Tropheus brichardi* (Sapp 2002) indicated no differences in NH_4 excretion rates between sedimented and reference sites. However, there are strong shifts in epilithic algal C:N associated with variation in benthic productivity (McIntyre unpublished), and algal P content is likely to vary in a similar fashion.

I hypothesized that productivity would significantly affect fish-mediated nutrient recycling. Specifically, I predicted a negative correlation between primary productivity and fish excretion rate because productivity is directly related to C:nutrient ratios. Fish consuming these low-nutrient algae must retain relatively more N and P than counterparts eating nutrient-rich algae, therefore nutrient excretion rates should be inversely related to the nutrient content of food resources (Sterner and Elser 2002). Thus, individuals feeding in a highly productive site should excrete less N and P than conspecifics at a less productive site.

Materials and Methods

Fish Collection

Eight *Tropheus brichardi* were collected at each of 8 sites over a 20-day period. Fish were captured by a snorkeler using a barrier net that did not entangle them. After being placed in

a transition bag of lake water for ~1 minute, each fish was transferred into a separate bag containing 1.5 liters of freshly filtered (Gelman A/E) lake water. Fish were incubated for ~30 minutes. Each incubation period was recorded to the nearest 30 seconds in order to determine excretion rate of NH_4 and SRP. Incubations occurred between 12 pm and 2 pm, to ensure similar physiological status of fish at all sites. Following incubations, dissolved oxygen (YSI 95) inside bags was measured for a subset of fish in order to verify that fish were not oxygen deprived. Two control bags containing 1.5 liters of filtered lake water without fish were also incubated and sampled to estimate background NH_4 and SRP.

Water Sample Collection and Analysis

Water samples were collected in 60 cc syringes using gloved hands, and transferred into well-rinsed HDPE sample bottles through a filter (Gelman A/E). From each incubation, one 10mL sample was diluted (1:1) with ultrapure water for NH_4 analysis and one 25 mL sample was collected for SRP analysis. Samples were stored on ice and analyzed on the day of collection. NH_4 was analyzed following the method of Holmes et al. (1999) using a Turner Designs Aquafluor fluorometer. SRP was analyzed by the HACH ascorbic acid rapid liquid method using a 5cm cuvette and a Thermospectronic Genesys 20 spectrophotometer. At each site, extra samples (one from a fish chamber and one from a control chamber) were analyzed for background fluorescence (NH_4) and matrix effects (NH_4 and SRP). Background fluorescence and matrix effects were negligible in every case. All nutrient concentrations were measured against freshly-prepared series of liquid standards.

Site Descriptions

Study sites covered a hypothesized primary productivity gradient near Kigoma (Thoms this volume). Coordinates are included in Table 1, and Figure 9 illustrates their locations along the shoreline. Nutrient dynamics at all sites were monitored throughout the study period (Corman this volume).

Statistical Analysis

Multivariate analysis of variance (MANOVA) was used to test differences among sites in NH_4 and SRP excretion rates. Separate univariate tests were then performed on NH_4 and SRP excretion rates and NH_4 :SRP to test for effects of site and fish wet mass. All variables were log transformed prior to analysis, and analyses were conducted using JMP-IN software.

Results

Mean SRP excretion rates ranged from 0.00546 to 0.0185 μmol per minute (Figure 1). There was a marginally significant difference among sites in SRP excretion rate ($F_{7,51} = 1.916$, $p = 0.086$). SRP excretion rate increased significantly with body mass ($F_{1,51} = 20.82$, $p < 0.001$), following a slope of 0.9226 (Figure 2). There was also a marginal negative relationship between SRP excretion and area-specific gross primary productivity (from Thoms, this volume).

NH_4 excretion rates ranged from 0.566 to 0.874 μmol per minute (Figure 4). There were significant differences among sites ($F_{7,51} = 18.39$, $p < 0.0001$), and NH_4 excretion rate increased

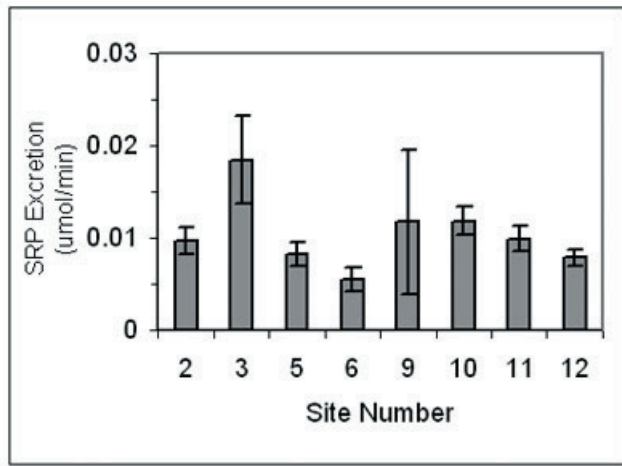


Figure 1: Spatial variability in SRP excretion rates across littoral sites

with body mass following slope of 0.3692 ($F_{1,51} = 94.74$, $p < 0.0001$; Fig. 5). Like SRP, NH_4 excretion rates decreased with increasing area-specific gross primary productivity (Figure 6).

Mean excreted N:P (NH_4 :SRP) varied across sites from 35.402 to 103.717 (Figure 7). There was a significant difference among sites in N:P ($F_{7,51} = 3.20$, $p = 0.007$). In addition, larger fish excreted at a significantly lower N:P ($F_{1,51} = 7.7$, $p = 0.008$; Fig. 8).

Discussion

The study demonstrates that a single species of fish, *Tropheus brichardi*, can show widely different patterns of nutrient excretion (Figs. 1 and 4). These patterns are likely to reflect differences in algal stoichiometry among sites. Comparing area-specific gross primary productivity (Thoms this volume) to molar excretion rates across sites indicates a general trend toward decreased nutrient excretion rates with increased primary productivity (Figs. 3 and 6). This interpretation is supported by the observation that C:nutrient of primary producers is often positively related to their productivity (Sterner and Elser 2002). Thus, homeostatic consumers such as fishes feeding on highly-productive algae may actually be nutrient-deprived, and consequently excrete relatively little excess N and P. The

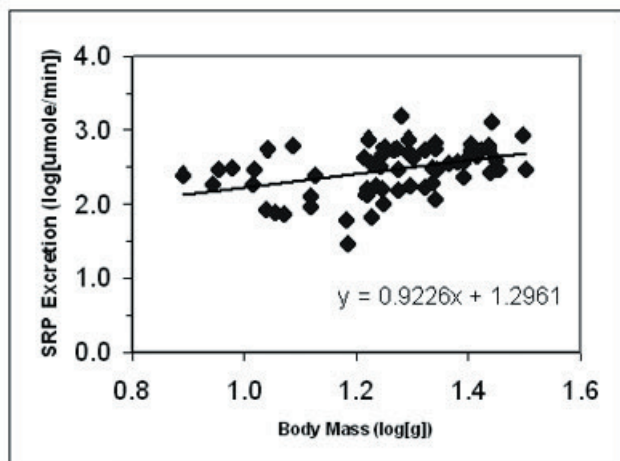


Figure 2: SRP excretion rate increased with body mass

fact that there were significant differences in excreted N:P among sites (Figure 7) suggests that spatial variation in algal N content and P content are decoupled. Variation in N:P may also have reflected the independent analytical noise from these two analyses.

There was also an overall positive association between body mass and excretion rates (Figs. 2 and 5). In both cases, the slope of the relationship was less than one, supporting the allometric principle that mass-specific nutrient excretion rates decline with body mass. The large difference in scaling exponents presumably reflects differential demand for N and P as a function of body size. For instance, P is invested largely in bones and ribosomes, which are required continuously as fishes grow, but N demand may decline more quickly because N-rich molecules are more important for tissue maintenance, which may decline with age and size. It is also possible

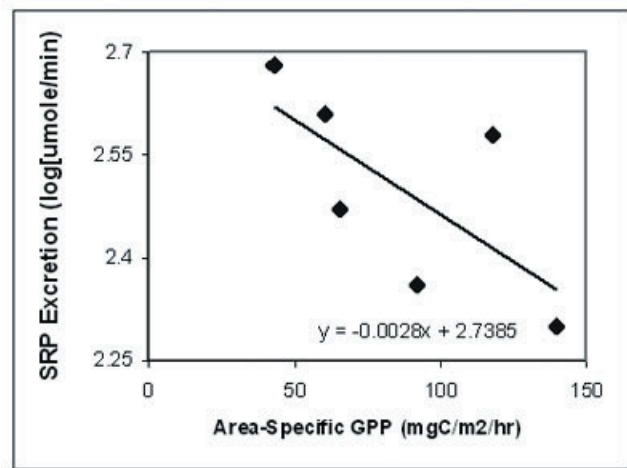


Figure 3: SRP excretion rate decreased with GPP across study sites

that there are differences among sites in the body nutrient composition of like-sized *Tropheus brichardi*, though this seems less likely (Sterner and Elser 2002).

In order to more accurately determine the relationship between algal nutrient content and excretion rates of benthic algal grazers such as *Tropheus brichardi* in Lake Tanganyika, carbon isotope and algal C:N:P data should be collected from the same study sites. Due to equipment limitations at TAFIRI and time limitations during the Nyanza Project, these analyses could not be performed during the current study. However, we have collected the needed samples, which await future analysis.

Future Research

Few studies have analyzed how species identity affects nutrient recycling rates and ratios (Vanni 2002). The littoral diversity of Lake Tanganyika offers many opportunities to investigate the ramifications of ecological stoichiometry at the ecosystem level. For example, interspecific variation in nutrient excretion may reveal differences in the identity of limiting nutrients. Many such issues are already under investigation (McIntyre unpublished), and this work will greatly expand understanding of the littoral ecosystem.

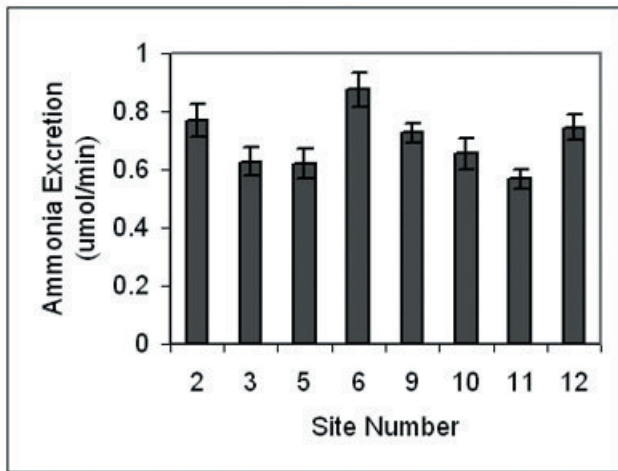


Figure 4: Spatial variability in ammonia excretion rates across littoral sites

Acknowledgements

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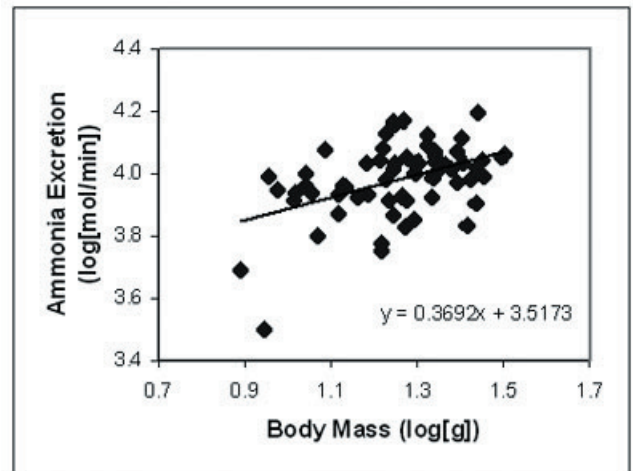


Figure 5: Ammonia excretion rate increased with body mass

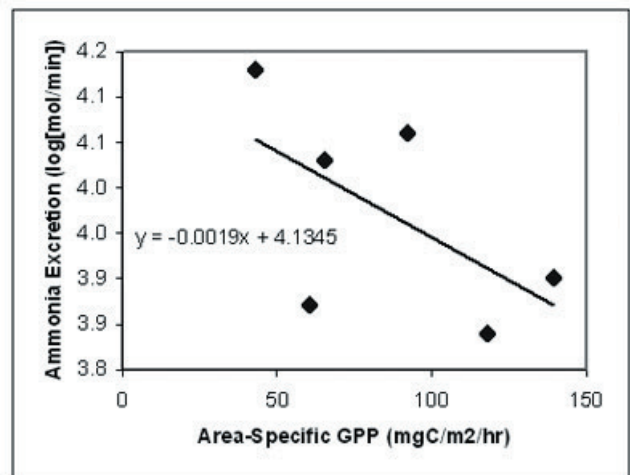


Figure 6: Ammonia excretion rate decreased with GPP across study sites

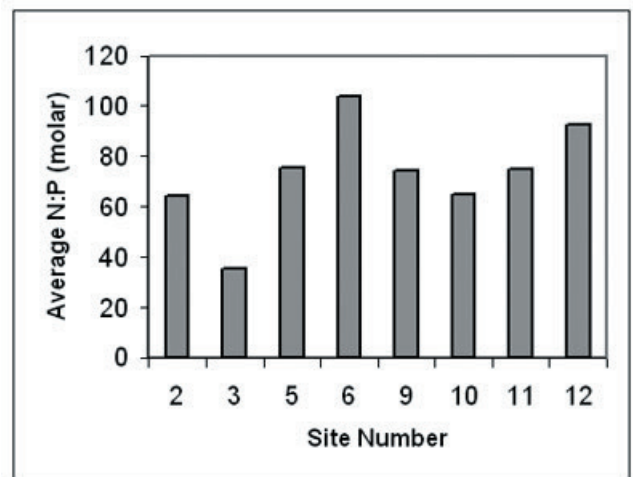


Figure 7: Spatial variability in excreted N:P across littoral sites

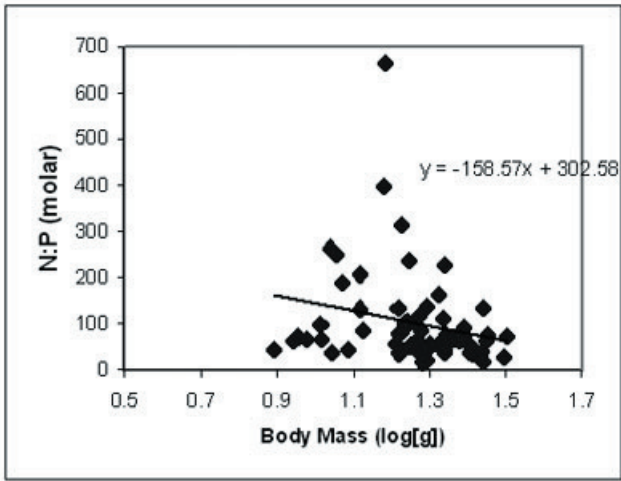


Figure 8: Excreted N:P decreased with body mass

Table 1: Study Site Locations	
Site Number	GPS coordinates
2	04°54.982'S, 29°35.766'E
3	04°54.804'S, 29°35.901'E
5	04°54.161'S, 29°35.682'E
6	04°54.003'S, 29°36.037'E
9	04°51.769'S, 29°36.509'E
10	04°50.956'S, 29°36.526'E
11	04°50.630'S, 29°36.445'E
12	04°50.191'S, 29°36.512'E

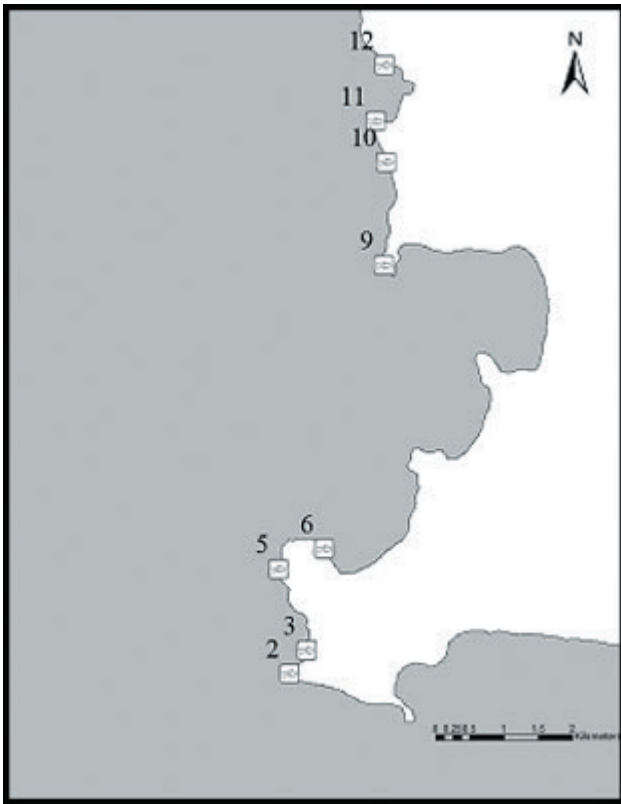


Figure 9: Location of study sites