

Indirect and direct effects of fish herbivory on nitrogen cycling in nearshore Lake Tanganyika

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INTRODUCTION

When external loading is small, as it is in Lake Tanganyika, the internal redistribution of nutrients can be important for ecosystem productivity. One conduit for this redistribution is fish. Research has been conducted on the transfer of nutrients into the pelagic or benthic ecosystems by benthic or pelagic fishes, respectively, but less attention has been paid to the recycling of nutrients by herbivorous fish in the littoral zone of lake ecosystems. In fact, many researchers have suggested that nutrient redistribution, or recycling of nutrients by fish, plays a small role in the overall nutrient budget of lentic ecosystems. However, in Lake Tanganyika, where the density of herbivorous fish is comparable to coral reef ecosystems, the effect of fish on recycling of nutrients should be more closely examined. Many factors can affect productivity in the nearshore environment, but the main objective of this research was to examine the effects of fish on nitrogen cycling in periphyton. More specifically, I examined (1) uptake of simulated fish excretion (i.e. NH_4) by plankton and periphyton communities and (2) the nitrogen turnover rate in periphyton protected and exposed to fish grazing in the littoral zone of Lake Tanganyika.

METHODS

Study Sites

Two sites were selected in the nearshore environment of Lake Tanganyika based on data indicating differences in benthic algal productivity (C/N and $\delta^{13}\text{C}$ from 2002, McIntyre unpublished; direct benthic productivity measurements, Thoms this volume). The first site, Jakobsen's Inner (04°54.804 S, 29°35.901 E), is highly productive, whereas the Katabe Bay (04°54.003 S, 29°36.037 E) site is low in benthic productivity. Surface water chemistry was monitored at both sites throughout the study period, and background and upwelling conditions were similar between them (Corman this volume). All samples were collected during the dry season (July 21- August 10, 2004), when strong southern winds prevailed.

¹⁵N Experiment

To measure the effects of herbivory on nitrogen turnover rates and cycling in periphyton, I used a ¹⁵N tracer experiment. The experiment involved two treatments: one that protected periphyton from grazing using a mesh exclusion, and another in which rocks were left uncovered to allow grazing. In previous studies, a 3.6 cm² mesh prevented grazing by medium and large sized herbivores (Solomon 2002), so that mesh size was used for exclusions.

Thirty cobbles (c.a. 6-10cm²) were collected from 3.0-3.5m depth at each site on July 28 and transported back to the laboratory in separate containers full of lake water, and quickly aerated. In each container, the water was replaced

with 40 L of fresh lake water, and 0.11 g of ¹⁵NH₄Cl salt (99 atom% ¹⁵N) dissolved in 50 ml of distilled water was added. The cobbles remained in the containers for approximately 36 hours to incorporate the ¹⁵N label. They were then returned to their original sites and placed at 3.0 m depth in three complete spatial blocks of five rocks from each treatment. Before placing cobbles back at the sites, mesh coverings were placed over both treatments for 24 hours to allow for leaching of ¹⁵N from the interstitial spaces in the periphyton matrix. After the initial leaching period the mesh was removed from the grazing treatment and the time zero (T_0) samples were collected. We sampled one cobbles per treatment per block at each site on five dates: Day 0, 1, 3, 5 and 7. During all five sampling periods, samples for stable nitrogen isotope analysis (and therein, C/N ratios) and chlorophyll *a* were collected.

The upward facing cobble was brushed to remove all periphyton material for stable isotope analysis, except for a 2 cm-diameter circle that was used for Chl *a* analysis. Algae were purified from the periphyton slurry using density centrifugation in colloidal silica (Hamilton and Lewis 1992), then rinsed three times and concentrated by centrifugation. The purified samples were placed in separate scintillation vials and dried at 60°C for 48 hours. Stable isotope analysis will be conducted at the U. Hawaii isotope biogeochemistry lab.

Chlorophyll *a* was measured from periphyton with the 2cm diameter circle. It was scrubbed from the rock, collected in a syringe, homogenized, and sub-sampled onto a Gelman A/E filter. The filters were frozen upon collection, and then placed in a cold, buffered 90% ethanol solution for an extraction period of 24 hours. Chlorophyll *a* was analyzed by fluorometry using a Turner Aquafluor.

NH₄ Uptake Measurements

Ammonium uptake rates by the periphyton and plankton communities were measured in the field at both sites. To measure uptake, a small NH_4 spike was introduced into transparent chambers that contained either (1) ambient water (hereafter the unfiltered treatment) or (2) ambient water plus a natural cobble substrate (hereafter the substrate treatment). Relatively flat substrates, with a large upward facing surface area, were collected from each same site immediately before each incubation. Chambers were 2.2 L clear, acrylic containers with an o-ring seal and rubber stopper in the lid. These chambers were placed at 3.0-3.5m depth during incubations. The spike was introduced by injecting 5 mL of concentrated NH_4Cl solution into each chamber through the rubber stopper using a syringe and long needle. This increased NH_4 concentrations by ~5 $\mu\text{g/L}$, which is comparable to excretion by an herbivorous fish over a 10-minute period (Hintz this volume). After the spike was added, and before collecting each sample, chambers were spun to homogenize internal nutrient chemistry. Sixty mL of water was removed from the chambers at each sampling using a syringe inserted through the rubber stopper of the chamber. Chambers were sampled after the NH_4^+ injection (T_0) and after 5, 10, 30, 60 and 120 minutes.

Water samples (20 mL) were filtered into HDPE amber bottles and placed on ice until analysis on the same day. We used a

modified version of the OPA-fluorescence method to measure NH_4 (Holmes et al. 1999). Standard curves (0-23 $\mu\text{g/L}$), matrix effects, and background fluorescence were run during every analysis. Uptake rates were adjusted for the dilution that accompanied sampling (i.e. removal of 60 cc of supplemented water and replacement with 60 cc of ambient water), and for the displacement of water by rock substrates. Non-linear regression analysis (SigmaPlot 8.0) was performed on NH_4^+ uptake rates.

RESULTS

^{15}N Experiment

Samples from the ^{15}N tracer experiment could not be analyzed in Kigoma. They will be reported at a later date.

NH_4 Uptake Measurements

Ammonium uptake was significantly greater in the substrate treatment than the unfiltered treatment at both sites ($p < 0.001$) (Figs. 1 and 2). The periphyton community exhibited a ten-fold

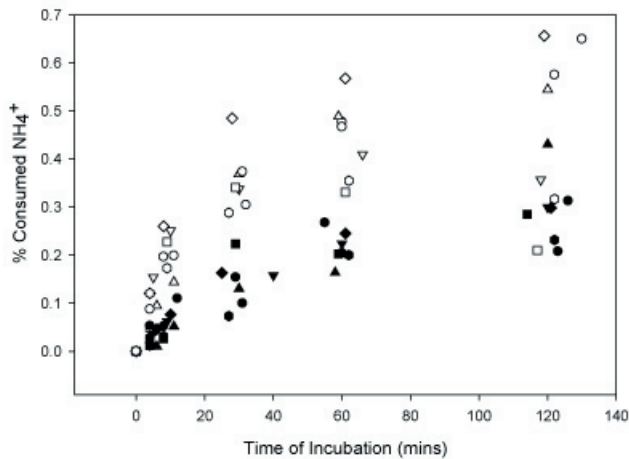


Figure 1: Ammonium uptake for unfiltered (closed symbols) and substrate (open symbols) treatments for both the Katabe and Jakobsen's Inner sites. Percent consumption is adjusted for differences in initial concentrations.

higher uptake rate relative to the plankton community (Fig. 3). Although not statistically significant, both the substrate and unfiltered uptake rates were greater at the Jakobsen's Inner site than at the Katabe site (Fig. 1, 2). In addition, uptake rates at Jakobsen's Inner were correlated with amount of NH_4 added to the chambers (4-7 $\mu\text{g/l}$; Fig. 4). No correlation was found at the Katabe site, though additions varied less than at Jakobsen's Inner.

DISCUSSION

In lake and stream ecosystems, it has been suggested that benthic algae may not be able to compete effectively with phytoplankton for limiting nutrients. Our results demonstrate that the periphyton community is able to rapidly exploit NH_4 from the water column. In fact, periphyton appeared to be more effective at utilizing water column NH_4 than littoral plankton.

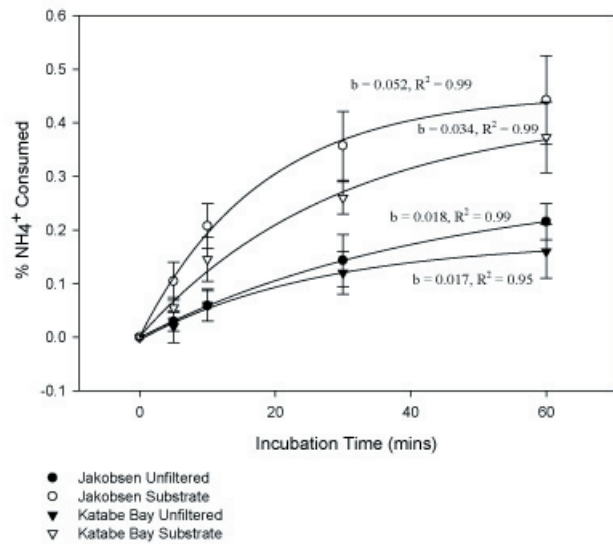


Figure 2: Average N uptake rates for unfiltered (closed symbols) and substrate treatments (open symbols) at both sites for incubation periods of 60 minutes.

This could allow them to quickly capitalize on locally-abundant excretion products from fish and other animals.

The N addition used in the uptake experiments was designed to mimic excretion by fishes, and was equivalent to only a few minutes of excretion by a single *Tropheus brichardi* (Hintz this volume). Many of the fish in Lake Tanganyika are territorial, suggesting that their consumption and excretion should be highly localized. Accordingly, recycling of N between herbivorous fish and periphyton could be a tightly coupled, positive feedback system. Gardening of periphyton by marine invertebrates and fish has been well documented, and could also be a characteristic of the littoral zone of Lake Tanganyika.

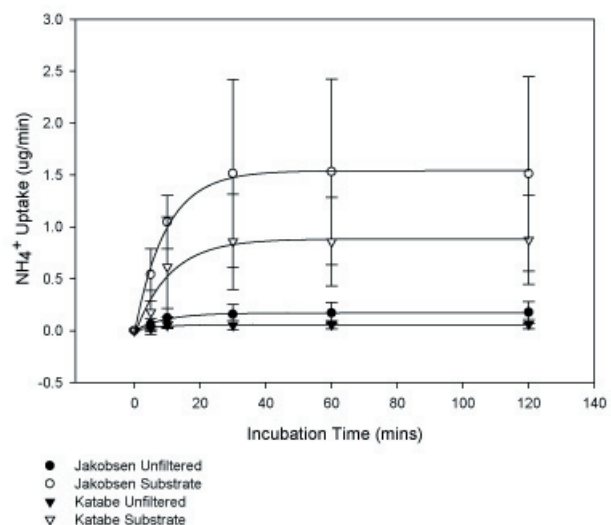


Figure 3: Volume-adjusted substrate N uptake rates (open symbols) relative to unfiltered treatments uptake rates (closed symbols).

LITERATURE CITED

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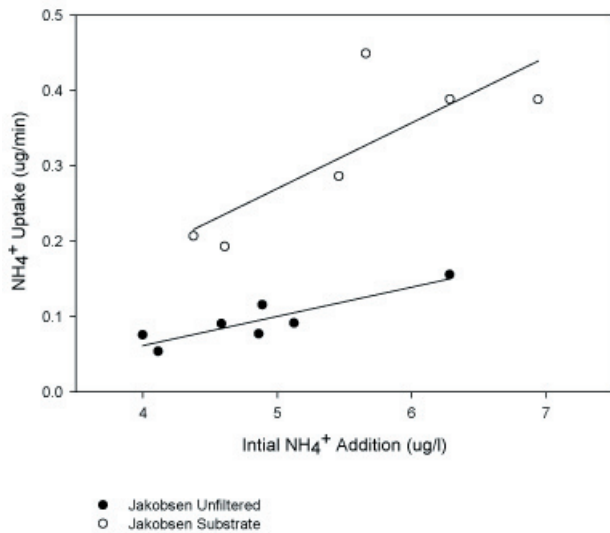


Figure 4: Comparison of initial NH₄⁺ addition to uptake rates at Jakobsen's Inner.

Fish grazing may also act to enhance nutrient availability to periphyton. Access to water column nutrients would be increased by reducing the density and thickness of periphyton mats, as well as by disturbing boundary layers along the substrate. In these ways, grazing could enable periphyton to compete more effectively for limiting nutrients. Our future results from the ¹⁵N turnover experiment will elucidate the strength of coupling between fish and periphyton.

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Site	NH ₄ ⁺ Uptake (ug l ⁻¹ day ⁻¹)
Jackobsen's Inner	
Unfiltered	98.1 ± 40
Substrate	414.9 ± 146
Katabe	
Unfiltered	72.3 ± 26.4
Substrate	234.5 ± 106.7

Table 1: Extrapolation of ammonium uptake rates for Jakobsen's Inner and Katabe sites from July 21-August 4, 2004