Trophic ecology of the benthic littoral of Lake Tanganyika: the role of grazers in determining algal biomass and productivity

Student: Christopher T. Solomon
Mentor: Dr. Ellinor Michel

Introduction

Trophic and community ecologists are interested in understanding the role of grazers in determining the standing stock and productivity of communities of primary producers. Lake Tanganyika is a large tropical lake renowned for its biodiversity and endemism across many taxa, including abundant grazing thiarid snails and cichlid fishes. The vast majority of the surface area and volume of the lake lies in the pelagic zone, yet most of the faunal biodiversity is restricted to the narrow band of littoral habitat along Tanganyika’s steep shore. Littoral zone communities have provided the laboratory for a great deal of work on evolutionary processes such as coevolution (West and Cohen 1996, West et al. 1991), radiation (e.g. Michel et al. 1992), and niche segregation (e.g. Hori et al. 1993), and have been the subject of recent interest in the effects of anthropogenic disturbance on Tanganyikan biodiversity (Cohen et al. 1993, Alin et al. 1999). Nonetheless, little is known about basic trophic dynamics of the littoral zone. We conducted a two-part investigation of littoral trophic ecology in Lake Tanganyika. First, we surveyed periphyton biomass at six depths in order to quantify the standing stock of benthic primary producers. Second, we used artificial substrates and exclusion cages to test the hypothesis that medium- and large-bodied grazers differ in their influence on benthic productivity and standing stock.

Methods

Periphyton biomass on natural substrates.—We measured periphyton biomass on natural substrates from depths of 20, 60, 100, 200, 400, and 600 cm along a 70 m stretch of rocky shore near Jakobsen’s Beach (4° 54.64’ S 29° 35.92’ E, ≈5 km S of Kigoma, Tanzania). Cobbles and small boulders with flat, upward-facing surfaces were collected by snorkeling and brought to the surface with a bottle cap (diameter=3.00 cm) forming a seal over the area to be sampled. Rocks were submerged in a dark box, transported to shore, and sampled for chlorophyll a (chl_a, a proxy for algal biomass). Using a wire brush and a squirt bottle, we first cleared all periphyton from around the cap and then sampled the area under the cap. The volume of sampled algae and rinse water was measured, and a subsample collected on a 25 mm glass fiber filter (Gelman Type A/E) using a syringe. The filter was immediately placed into 8 mL of chilled 90% ethanol and kept in the dark for 1 d to extract chlorophyll (Nusch 1980). Spectrophotometric absorbance of the extract was measured (Spectronic 21D, 1 cm path length, Spectronic Instruments) to determine chl_a. We regressed area-specific chla on depth after excluding two outliers from the data. All analyses were performed using SYSTAT (Version 7.0, SPSS Inc., 1997). Light penetration in the littoral zone was measured using an underwater radiation sensor (LI-193SA, LI-COR, Inc., Lincoln, Nebraska, USA) to determine the light extinction coefficient, k, and assess the availability of light with depth. At depths ranging from 1-6 m we took replicate readings of irradiance at the surface and at depth, calculated k for each replicate, and then determined the mean value of k. We repeated this procedure at 10:00 and 17:00 on 3 August 2001 to assess diel differences in the coefficient of light extinction in the littoral zone.

Effects of grazers.—Algivorous fish and snails are both abundant and diverse in the littoral zone of Lake Tanganyika, but their effects on ecosystem processes of the periphyton community are relatively unknown. We conducted a field experiment to examine the short term effects of these two taxa on periphyton biomass and productivity. Clay flower pots (surface area ≈ 128.5 cm²) were enclosed in plastic fencing (mesh size ≈ 1x1.5 cm) to exclude medium- and large-bodied grazers, and incubated in the lake at 2-2.5 m depth for 16 d to allow colonization by periphyton. On 30 July 2001, pots were transported to shore submerged and in the dark, blocked in groups of three based on incubation location, and haphazardly assigned to one of three treatments: small mesh exclusion cage, large mesh exclusion cage, and open. Pots assigned to the small mesh treatment retained their 1x1.5 cm incubation cages. Pots in the large mesh treatment had their incubation cages replaced with a larger mesh exclusion cage (mesh size ≈ 1.6x2.3 cm). Pots in the open treatment were removed from their incubation cages and not given new cages. These treatments and mesh sizes were chosen such that small-bodied grazers (e.g. shrimp and insects) had access to all pots, medium-bodied grazers (snails, small crabs, and small fishes) had access to large mesh and open pots, and large-bodied
grazers (large fishes) had access only to open pots. By 18:00 all pots were affixed to large cobbles and replaced in
the lake at 3 m depth, with each block resting on a different flat rock along 25 m of shoreline.

On 2 August (blocks 1-6) and 3 August (blocks 7-15), we removed pots from the water and used dark and light
incubations to determine respiration and net primary production. Blocks were brought to shore one at a time, where
pots were cut free from their cages and anchoring cobbles. Incubations were run in clear plastic 2.19 L chambers
with an O-ring seal and a stoppered hole in the lid. We placed each pot in a chamber full of fresh lake water,
measured initial dissolved oxygen (DO) and temperature with a meter (YSI95, YSI), stopped the chamber, and
placed it in an opaque plastic bag at 3 m depth. All three chambers from a block were incubated in the same bag,
along with one blank chamber that contained lake water but no pot. The entire bag was brought back to shore after
30-60 min., and chambers were removed one at a time, unstoppered, and measured again for DO and temperature.

After refreshing the water in the chamber and taking a new initial DO measurement, we placed chambers back in the
previous location for 30-70 min. of light incubation followed by another DO measurement. Oxygen evolution or
consumption in each chamber was calculated from the DO measurements and the volume of water in the chamber,
corrected within each block by the oxygen consumption or generation in the blank. Net primary production (NPP)
was calculated in mg C m$^{-2}$ hr$^{-1}$ as NPP = $Vk(D_1 - D_0) / tA$ where $V=2.19$ L, the volume of the incubation chamber,
k=0.6661, the number of milligrams of carbon produced per mg of oxygen, $D_1$ and $D_0$ are respectively the final and
initial dissolved oxygen readings in mg*L$^{-1}$, t is the time in hours between $D_1$ and $D_0$, and $A=0.01285$, the surface
area of the clay pot in m$^2$. Respiration was similarly calculated from the dark incubations, and subtracted from NPP
to obtain gross primary productivity, GPP. At the end of the day all pots were transported back to the lab and
sampled for chla using the methods described above. Biomass-specific production of the periphyton was calculated
as GPP/chla for each pot. We used randomized blocks MANOVA to analyze respiration and NPP data, and then
used univariate randomized blocks ANOVA with Bonferroni-corrected multiple comparisons to examine treatment
effects on NPP, periphyton biomass, GPP, and biomass-specific GPP. Biomass-specific GPP data were log
transformed to correct problems of unequal variance before analysis.

Results

Periphyton biomass on natural substrates.—Chlorophyll a values measured on natural substrates ranged from 9.38 ±
1.26 µg cm$^{-2}$ (mean ± SE) at 20 cm depth to 3.38 ± 0.28 µg cm$^{-2}$ at 600 cm. Both the mean and the variance of
periphyton biomass decreased with depth; most of the decrease occurred in the first meter of water (Fig. 1). The
regression equation $y = 0.330 z^2 - 2.936 z + 9.271$, where $y$ is chla in µg cm$^{-2}$ and $z$ is depth in meters, explains
52.2% of the observed variation in periphyton biomass. The coefficient of light extinction measured in the littoral
zone was 0.23 at 10:00 and 0.32 at 17:00, reflecting the increased afternoon turbidity associated with daily wind-
duced mixing.

Effects of grazers.—Casual observations on experimental pots indicated that treatments were probably grazed by the
intended size ranges of herbivores. Fish (Ophthalmotilapia ventralis, Cichlidae) and adult snails (Lavigeria coronata,
L. nassa, and L. grandis, Thiaridae) were observed grazing on open pots, the fish within 1 h of the start of the
experiment. One pot in the large mesh treatment had a large snail grazing scar on its surface at the end of the
experiment, although the snail was no longer on the pot. Individual crabs (Platytelphusa polkadot, Platytelphusidae,
a fairly small species that probably grazes algae) were found underneath the anchor rocks of several pots when they
were removed from the lake. Juvenile snails (Reymondia, Lavigeria spp., ~2-3 mm length) were found on some
pots in all treatments, particularly on exclusion pots.

The biomass of periphyton on artificial substrates incubated at 3 m and protected by exclusion cages was similar to
that found on natural substrates at similar depths (large mesh pots 3.57 ± 0.38 µg chla cm$^{-2}$ mean ± SE, small mesh
pots 4.00 ± 0.42 µg chla cm$^{-2}$; Figs. 1-2). There was a significant treatment effect on chla ($F_{2,26}$=13.80, p<0.001),
whereby allowing access by the full community of grazers significantly reduced periphyton biomass (p≤0.001 for
both of the pairwise comparisons of the open treatment with the other treatments). Multivariate analysis of
respiration and NPP revealed significant block (Wilks’ lambda=0.168, $F_{2,26}$=13.76, p<0.001) effects. The significance of the block effect was driven by the NPP response,
as there was no block effect on respiration in a univariate analysis ($F_{14,26}$=1.38, p=0.225). Gross primary productivity
was significantly lower in the open treatment (115 ± 11 mg C m$^{-2}$ h$^{-1}$) than in either the large mesh (183 ± 11 mg C
m$^{-2}$ h$^{-1}$) or the small mesh (198 ± 9 mg C m$^{-2}$ h$^{-1}$) exclusion treatments ($F_{2,26}$=37.09, p=0.001; Fig. 3). However,
biomass-specific GPP showed the opposite pattern, with a significantly higher mean in the open treatment than in
Figure 1.

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Chl (ug/cm²)

Depth (cm)
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Figure 2.

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Chl (ug cm⁻²)
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Figure 3.

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GPP (mg C cm⁻² hr⁻¹)
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Figure 4.

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GPP (mg C ug chl a⁻¹ hr⁻¹)
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either of the exclusions ($F_{2,26}=9.25, p=0.001$; Fig. 4). There were no significant differences between the two exclusion treatments in any of the measured response variables.

**Discussion**

The pattern of decline of periphyton biomass with depth (Fig. 1) is very similar to that described by Miller (2000) at the same site, though my calculation of biomass is an order of magnitude higher at every depth. Although periphyton biomass in the benthic littoral of Lake Tanganyika has rarely been quantified, it seems unlikely that dry-season standing stock of periphyton could fluctuate so widely between years. Variation in depth explains only 52.2% of the observed variation in chl$_a$, which suggests that light availability, which decreases as a constant function of depth, is not the sole factor controlling periphyton biomass.

The results of the grazer exclusion experiment indicate that grazing fish strongly limit standing stock and gross primary productivity of epilithic periphyton in the littoral zone of Lake Tanganyika. Large-bodied fish were the only grazers that could access open pots but not exclusion pots, and periphyton biomass and GPP both decreased by more than 50% in the open treatment compared to the exclusions (Figs. 2-3). In contrast, the lack of any significant differences between small and large mesh pots indicates that if medium-bodied consumers such as crabs and snails have any significant effects on periphyton production and biomass, they are not manifested at the time scale of this experiment. The design of this experiment does not allow us to assess the role of small-bodied grazers, which are important in some systems (e.g. Pringle ____). With that proviso in mind, we nonetheless propose that grazing fishes, which are large-bodied, abundant, and highly mobile, are the dominant consumers of littoral periphyton.

The periphyton community on open pots had relatively low biomass but high productivity (Fig. 4), a common characteristic of grazed benthic algae (Steinman 1996). Similarly, the pelagic zone of Lake Tanganyika is characterized by low standing stocks but high productivity (Hecky 1991). Yet while high-end estimates for the phytoplankton biomass and productivity of the pelagic are respectively 2.1 mg chl$_a$ m$^{-3}$ and 4.6 mg O$_2$ m$^{-3}$ d$^{-1}$ (Raini and Isumbisho 2001), the lowest estimates from the present study for littoral periphyton biomass (from natural substrates at 6 m) and productivity (from artificial substrates at 3 m) are respectively 33.8 mg chl$_a$ m$^{-2}$ and 104 mg O$_2$ m$^{-2}$ h$^{-1}$ (note units). We posit that this tremendous benthic productivity has helped to fuel the rapid evolutionary processes of Lake Tanganyika by providing nutrition for an exceptionally dense consumer community. Packing so many consumers into a narrow band of habitat likely intensifies pressures for sexual selection and trophic differentiation. Furthermore, we suggest that production in the littoral zone may be an important part of nutrient and energy flows at the whole-lake level. Continued study of littoral zone trophic ecology is necessary to examine these processes.

**Recommendations for Further Study**

(1) Analyses presented in this extended abstract should be rerun before publication in a refereed journal. In particular, model assumptions should be more thoroughly checked, and random factors should be treated as such (all were treated as fixed for these analyses). (2) It is imperative to develop an understanding of the composition of the periphyton community and how it responds to variation in light availability, grazing pressure by different taxa, and so forth. It would be great to get an algae expert to the Nyanza Project as a guest researcher to help develop sampling protocols and a taxonomic key. (3) Gather more supplementary data on big field experiments. Have students sit down before they run an experiment and brainstorm possible weird results they could get, and then list what data sets they would want to help explain these weird results. Then collect at least some of this data—better a little extra field work than an inability to explain what’s going on after you have put a lot of work into an experiment.

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References
Pringle, C.

Figure Captions

Figure 1. Biomass of periphyton (measured as µg chl a cm⁻²) on natural substrates along the rocky shore at Jakobsen’s Beach, Lake Tanganyika.

Figure 2. Biomass of periphyton (measured as µg chl a cm⁻²) on artificial substrates exposed to 2-3 d of grazing by different grazers. Treatment names refer to small mesh exclusion caging, large mesh exclusion caging, and open/no caging; cartoons indicate which grazers have access to the substrates. Treatments marked with the same letter are not significantly different.

Figure 3. Area-specific gross primary productivity (GPP) on artificial substrates exposed to 2-3 d of grazing by different grazers. Treatments marked with the same letter are not significantly different.

Figure 4. Biomass-specific gross primary productivity (GPP/µg chl a) on artificial substrates exposed to 2-3 d of grazing by different grazers. Treatments marked with the same letter are not significantly different.