

# Do gastropod abundances and distributions vary in relation to primary productivity and site complexity?

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## Introduction

Population ecology incorporates a variety of foundational tenets that aid in understanding community structure and biodiversity of organisms in the natural world. For example, it has been observed that increasing the habitat and environmental complexity is correlated with increasing species diversity (Rosenzweig, 1995). Lake Tanganyika, in central East Africa, represents an ideal system to test this canon. The rocky littoral zone of Lake Tanganyika supports a highly diverse ecosystem, including numerous species of the endemic gastropod clade *Lavigeria*. Although *Lavigeria* is the most common gastropod on the rock surfaces and the focal organism of several studies examining sedimentation, speciation, and predation, the diversity and abundance patterns of this species flock remain poorly understood (Michel *et al.*, 2003).

This study is one part of a collaborative effort to test two alternative hypotheses for the patchy distributions of gastropod species at rocky sites around Kigoma Bay, Tanzania. I am testing niche explanations for species' abundances and distributions, whereas Meyer's study (this volume) applies the same data to test predictions from neutral theory along a spatial scale of continuous and discontinuous habitats. Niche distribution perspectives rely on abiotic and biotic factors controlling not only an individual's fitness but also species' distributions (Begon & Mortimer, 1981). I analyzed gastropod distributions by relating environmental factors of primary productivity and habitat complexity to snail diversity. Measurements of benthic primary productivity were generated using chlorophyll *a* concentrations and dissolved oxygen fixation, and gross primary productivity was derived in collaboration with Thoms (this volume) and Vadeboncoer (in progress). Site complexity was explored through measures of substrate heterogeneity, shoreline aspect, and benthic rugosity. These environmental factors were evaluated to test the hypotheses that sites with high benthic primary productivity, high substrate heterogeneity and high rugosity will support increased diversities and abundances of gastropods.

## Methods

### Site Selection

Research was conducted in the Kigoma region of Lake Tanganyika, Tanzania between July 20-Aug 2, 2004. Twelve sites were selected along a longitudinal gradient beginning south of Kigoma and extending north of the Gombe Stream National Park. Beginning in the south, sites included Muzungu Beach (4°55.057S, 29°35.911E), Jacobsen's South (4°54.982S, 29°35.766E), Jacobsen's Central (4°55.804S, 29°35.901E), Jacobsen's North (4°55.516S, 29°35.822E), Katabe South (4°55.161S, 29°35.682E), Katabe Inner (4°55.003S, 29°36.037

E), Hilltop (4°53.227S, 29°36.795 E), Euphorbia (4°50.956S, 29°36.526 E), Kalalangabo South (4°50.630S, 29°36.445 E), Kalalangabo North (4°50.191S, 29°36.512 E), Mitumba (4°37.977S, 29°37.898 E), and Mwamgango (4°36.960S, 29°38.290 E). All sites consisted of rocky substrate and were sampled at 5m depth in order to sample the greatest density and diversity of *Lavigeria* (Michel, 2000). Rocky substrate was defined as benthic habitat dominated by cobbles, boulders or large bedrock outcrops. In order to obtain the most accurate and useful measurements of benthic productivity, algal biomass, and bathymetry, both the "Benthic team" and the limnology team sampled the same 10 sites. Two additional sites were sampled in the Gombe Stream region for this study to allow for temporal comparison with Gombe Stream sites sampled in 2003.

### Quadrat Sampling

Five 1m<sup>2</sup> quadrats were sampled at each site. Methodology was patterned after Barrett *et al.* (2003) where each quadrat was placed 10m apart along a depth contour of 5m. All live snails larger than 5mm were collected from each quadrat. In order to maintain consistent areas for density calculations, only upward facing surfaces were sampled. Sifting through sandy substrate or turning over rocks was avoided to maintain a 1m<sup>2</sup> sample area. All collected snails were returned to TAFIRI laboratories for species identification and measurements. Snails were scrubbed clean and identified. Measurements were taken using Mitutoyo® digital calipers of total length, width, lip thickness and number of scars. Ontogenetic stage of each specimen was categorically recorded as adult, sub-adult or juvenile based on lip thickness and other adult modifications. Biomass of all individuals was calculated based on total shell height using the formula biomass = 0.2208e<sup>0.996</sup>[shell height (mm)] (from Socci, pers. comm. and Barrett *et al.*, 2003). Total biomass (g/m<sup>2</sup>) was summed per site.

### Biodiversity

Species presence at a site was determined using benthic "sweeps," based on the methodology from Barrett *et al.* (2003). Their protocol was modified to a single 20 minute sweep conducted by 3 divers. Target specimens included all littoral snails greater than 5mm in height. The sweep began at 10m and ascended to the surface following the benthic contours. Divers were placed 5 m apart along a randomly selected portion of the site. Substrate was examined for live species and included searching through sandy substrate and the underside of rocks. A total list of species present at each site was generated as an indication of species richness. Species abundances were determined per species at each site and log<sub>2</sub> transformed (per PAST© statistical package recommendation) to account for variable sample sizes of snails between sites and habitat patchiness observed in the snail communities. Based on these standardized abundances, diversity indexes of Fisher's Alpha, Shannon H, and Simpson 1-D were calculated using PAST© statistical package. These indices combine both evenness and abundance data while controlling for small sample sizes.

### Site Complexity

Substrate complexity of the rock substrate was measured at three different spatial scales. First, at the coarse scale, a compass was used to supply site aspect at a heading perpendicular to the

shoreline. Secondly, at moderate scale, spatial heterogeneity of the substrate was measured using rugosity measurements. Three separate measurements over a constant linear distance were recorded. Rugosity was calculated as the total length (TL) of metal chain laid flush with the benthic contours to a standard 5m linear length (LL) along a 5m depth transect (TL:LL) (Chapman, 2000). Third, substrate composition was calculated using the point intercept method. Digital photographs of each quadrat were taken to assess percent cover of substrate grain size (Coyer, *et al.*, 1999). The Wentworth scale was used to classify substrate as fine sediments, sand, pebbles, cobbles or boulders (Barrett *et al.*, 2003.) A 25-point intercept grid was overlaid on the digital quadrat photos using Adobe Illustrator and substrate types were recorded at each intersection. The percent cover values for each quadrat were converted into a single indexed value used by Barrett *et al.* (2003) to represent substrate heterogeneity.

### Benthic Productivity

Benthic algal productivity was approximated using chlorophyll *a* as a proxy (Gilbert, 2003). A known area of benthic algae was scrubbed off the upward facing of small cobbles taken from each site. Rocks were collected from 2m depths and included six replicates. The removed algae were suspended in a 60ml syringe, agitated to improve uniformity, and sub-sample of 5ml filtered through a GF 25mm filter. Filters were cold extracted in 10ml of a 90% ETOH solution for a 24h period. Samples were acidified using a 0.1M HCl acid source and run on a Turner designs Aquasense handheld fluorometer. Methods for quantifying benthic gross primary productivity (GPP) were conducted by the Nyanza limnology team and can be found in Thoms (this volume).

## Results

### Productivity

Benthic algal productivity and species diversity were compared with linear regressions using the JMP IN (v.4.0.4) statistical package. Significant inverse relationships were found between Shannon H diversity index and benthic algal biomass ( $p=0.0491$ ,  $R^2 = 0.404$ ) (Fig 1a). A second linear regression showed a marginally significant inverse relationship between

species richness and benthic algal biomass (Fig. 1b). GPP showed a strong unimodal relationship with species richness ( $R^2 = 0.6524$ ); species number increases as GPP approaches 100 (mg C / m<sup>2</sup>-h), then decreases as productivity continues to rise (Fig 2). However, a similar unimodal pattern was not present in total biomass per site when related to GPP.

### Site Complexity

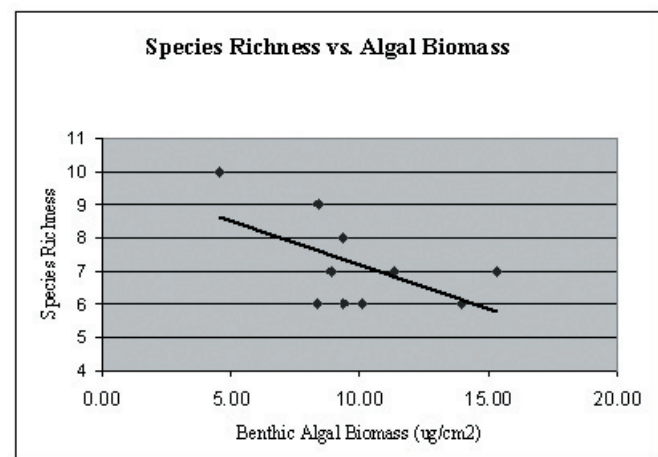
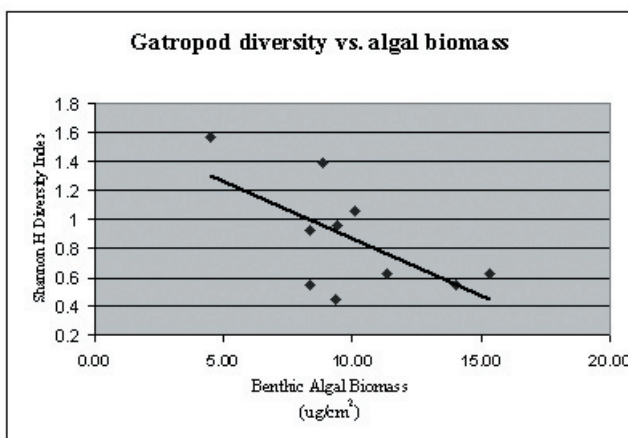
A linear regression compared Simpson's 1-D diversity variations to rugosity. A strong linear correlation is shown in Fig 3 ( $p=0.0025$ ;  $R^2 = 0.6138$ ) relating increases in rugosity to increases in the diversity. Since Simpson's 1-D diversity index is a calculation based on evenness and species richness of a sample, and there was a weak relationship between rugosity and species richness, a second regression was performed to compare species evenness to habitat rugosity (Fig. 4). This trend exhibits greater correlation and higher statistical significance than the diversity index alone ( $R^2 = 0.750$ ;  $p=0.0003$ ). Shannon's diversity was also compared across a shoreline aspect. Sites were grouped into NE, NW, SW, and W facing slopes and compared using a one factor ANOVA ( $p=0.0499$ ; Fig. 5). A second ANOVA using Shannon's diversity followed by a LSMeans Tukey test showed significant differences for substrate heterogeneity index values of 2 and 3 ( $p=0.0382$ ).

### Cluster Comparison

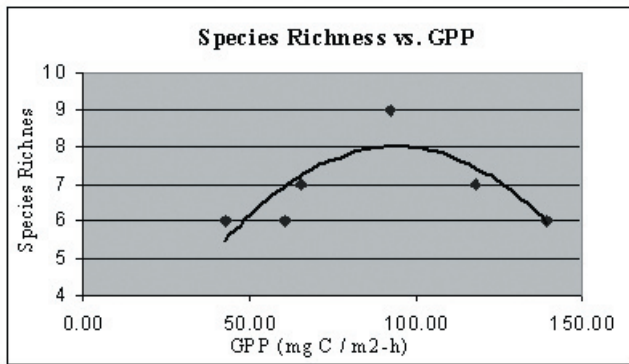
Multivariate cluster analysis performed using PAST statistical package were completed on each environmental factor examined in this study to compare with community distributions established in Meyer (this volume). Paired cluster analyses were completed with benthic algal biomass, rugosity, substrate heterogeneity, and shoreline aspect using the Morista similarity measure for consistency with Meyer. A similar distribution pattern can be seen between the diversity cluster and the substrate heterogeneity cluster (Fig. 6).

## Discussion

The results of this study suggest the several environmental factors play an important role in structuring species distributions and abundances. In relation to this complexity, gastropod



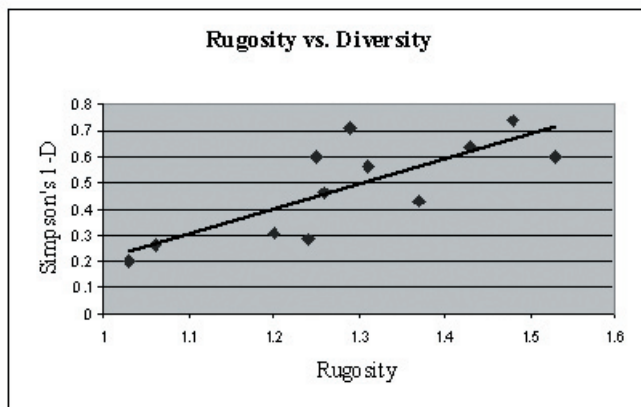
**Figure 1:** Linear regressions of a) gastropod diversity ( $R^2 = 0.404$ ) and b) species richness ( $R^2 = 0.332$ ) to benthic algal biomass



**Figure 2:** Scatter plot of gross primary productivity (GPP) compared to species richness ( $R^2 = 0.6524$ )

distributions may be realized niche dependent. Productivity is generally recognized as a significant abiotic factor in determining community structure (Begon and Mortimer, 1981). Preliminary results from this study show interesting trends between benthic algal biomass and GPP in relation to gastropod diversity. Contrary to my initial hypothesis, increased benthic algal biomass leads to decreases in both diversity and species richness. This suggests that competitive exclusion may occur in areas of increased food source and production. Further study is needed to verify that increases in benthic algal biomass result in population growth of successful competitors at the expense of poor competitors. Competitive exclusion may also increase with high GPP values (Fig. 6). Additional increases in GPP led to decreases in species richness. This unimodal productivity pattern concurs with Rosenzweig's conception of species richness across a comprehensive productivity gradient - often diversity declines after productivity grows beyond a certain point. Several animal communities have shown this pattern, including marine benthic gastropods (Rex, 1981). While biomass often correlates to productivity, this is not always the case (Rosenzweig, 1995). Therefore, while there is a strong unimodal pattern for gastropods regarding productivity, it is consistent within this explanatory framework to see no similar pattern in gastropod biomass.

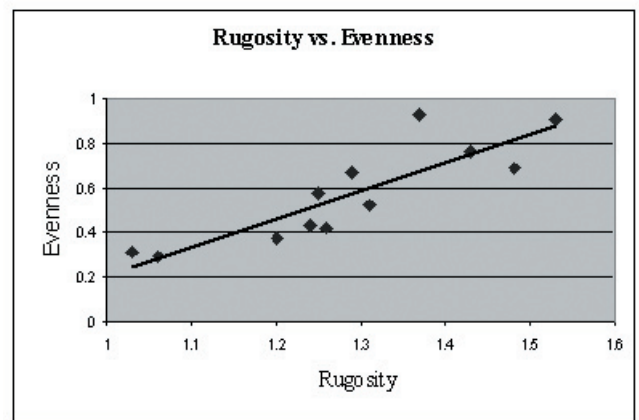
Site complexity is also related to gastropod distributions. Changes in shore aspect, rugosity and substrate heterogeneity show significant trends with gastropod diversity. Areas of greater diversity include sites with high rugosity, perhaps



**Figure 3:** Linear regression of Simpson's 1-D diversity index to rugosity variations ( $R^2 = 0.6138$ )

indicating that more complexity of rocky substrate increases the potential niche exploitation for various species of gastropod. Additionally, N and NW facing slopes exhibited high diversity. This paralleled results found in 2003 (Barrett *et al*, 2003.) for the Kigoma region and should be teased apart further to understand what physical parameters associated with N/NW facing shorelines positively correlates with gastropod densities. Lastly, substrate heterogeneity may play a key role in determining snail distribution. The similarity between cluster comparisons of snail diversity and substrate heterogeneity across sites is remarkably similar. Additionally, from personal observation, substrate type appears to play an important role in the species of gastropods found on the rock surfaces.

Further research is needed to strengthen the relationships presented in this paper. Increased sampling would improve accuracy and robustness of results. An attempted measure of water motion, using the 'clod card' technique (Doty, 1971), was



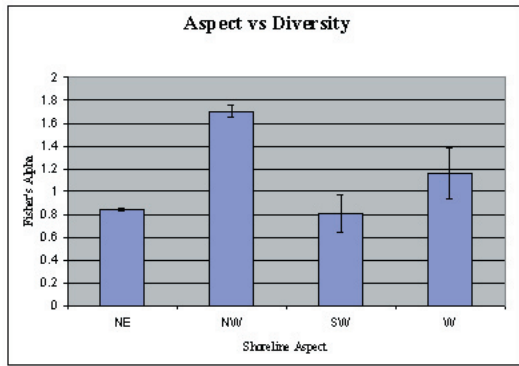
**Figure 4:** Linear regression of evenness to rugosity variations ( $R^2 = 0.750$ )

attempted during this field season but was unsuccessful due to logistical constraints. It would be interesting to repeat the clod card procedure to establish a greater understanding of the impact of shoreline aspect, nutrient availability and site benthic productivity.

Ideally, this report will serve a framework to guide more detailed hypotheses of environmental complexity shaping gastropod distributions in the subsequent Nyanza field seasons. Understanding gastropod distributions may serve as a model for other lake organisms, valuable for preserving endemic biodiversity and sustaining ecologically important species. By emphasizing the importance of niche distribution and abiotic environmental factors in *Lavigeria* abundances, we can better understand the potential damage of anthropogenic inputs and habitat modifications on other species' populations.

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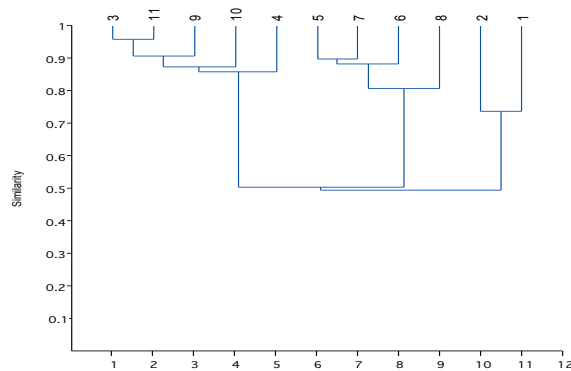
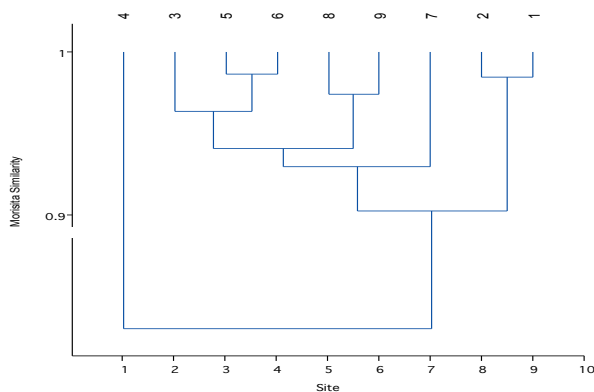
Source	DF	Sum of Squares	Mean Square	F Ratio	Prob > F
Model	3	0.8366383	0.278879	4.0684	
Error	8	0.5483867	0.068548		
C. Total	11	1.3850250			0.0499

**Figure 5:** Shoreline aspect and gastropod diversity. Analysis of variance results showing significance

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**Figure 6:** Multivariate paired cluster analyses. Left, similarity of substrate heterogeneity between sites. Right, similarity of gastropod diversity between site. Site numbers are in order of presentation in the text, with the southernmost site as number 1, northernmost as number 10.