
Individual- and Assemblage-Level Effects of Anthropogenic Sedimentation on Snails in Lake Tanganyika

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Abstract: *Human impacts on aquatic biodiversity are often measured at the assemblage or community level, although it has been suggested that individual-level measures are more sensitive. We evaluated the effects of anthropogenic sedimentation on endemic snails in Lake Tanganyika, East Africa, by comparing assemblage-level (i.e., species richness, evenness, and abundance) and individual-level (i.e., frequencies of predation and parasitism, fecal organic content, life history) data between sediment-disturbed and reference sites. Previous studies have indicated that sedimentation kills snails and reduces mollusc diversity in this system, but we found little evidence of changes in species richness, evenness, or snail abundance at the levels of sedimentation recorded. In contrast, individual-level data revealed a variety of differences associated with sedimentation. Frequencies of shell scarring by predatory crabs and castration by parasitic trematodes were significantly lower at disturbed sites, indicating shifts in interspecific interactions. Snails ingested large amounts of inorganic sediments at disturbed sites, suggesting a reduction in food quality. In addition, sedimentation was associated with a large downward shift in size distribution within some species and reproduction at smaller size. These strong patterns in individual-level data contrast with the lack of effects at the assemblage level. We argue that incorporating individual-level measures will often enhance the sensitivity of impact surveys and may reveal effects of disturbance on important interspecific interactions.*

Key Words: crab, *Lavigeria*, life history, parasitism, predation, trematode

Efectos a Nivel Individual y de Ensamble de la Sedimentación Antropogénica sobre Caracoles en el Lago Tanganyika

Resumen: *Los impactos humanos sobre la biodiversidad a menudo son medidos a nivel de ensamble o comunidad, aunque se ha sugerido que medidas a nivel individual son más sensibles. Evaluamos los efectos de la sedimentación antropogénica sobre caracoles endémicos en el Lago Tanganyika, África Oriental, mediante la comparación de datos a nivel ensamble (i. e., riqueza de especies, equitabilidad y abundancia) y a nivel individual (i. e., frecuencias de depredación y parasitismo, contenido fecal orgánico, historia de vida) entre sitios perturbados por sedimentos y sitios de referencia. Estudios previos han indicado que la sedimentación mata a los caracoles y disminuye la diversidad de moluscos en este sistema, pero encontramos poca evidencia de cambios en la riqueza de especies, equitabilidad o abundancia de caracoles en los niveles de sedimentación*

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Paper submitted October 3, 2003; revised manuscript accepted April 29, 2004.

registrados. En contraste, los datos a nivel individual revelaron una variedad de diferencias asociados con la sedimentación. Las frecuencias de cicatrices en la concha por cangrejos depredadores y de castración por trematodos parásitos fueron significativamente menores en los sitios perturbados, lo que indica cambios en las interacciones interespecíficas. Los caracoles ingirieron grandes cantidades de sedimentos inorgánicos en sitios perturbados, lo que sugiere una reducción en la calidad del alimento. La sedimentación también estuvo asociada con un notable cambio descendente en la distribución de tallas en algunas especies y con la reproducción a menor talla. Estos patrones evidentes en los datos a nivel individual contrastan con la carencia de efectos a nivel de ensamble. Argumentamos que la incorporación de medidas a nivel individual incrementa la sensibilidad de evaluaciones de impacto y puede revelar efectos de la perturbación sobre interacciones interespecíficas importantes.

Palabras Clave: cangrejo, depredación, historia de vida, parasitismo, trematodo

Introduction

Most studies of human impacts on aquatic biodiversity emphasize changes in community- and assemblage-level measures such as taxon richness or evenness (e.g., Resh & Jackson 1993; Johnson 1998). This focus reflects a variety of considerations (Warwick 1993; Attrill & Depledge 1997), such as the efficiency of addressing many species simultaneously and the prioritization of conserving maximal species diversity in most conservation efforts. In addition, it is usually assumed that changes in the ecology of individuals will have observable effects at the assemblage and community levels.

Despite these appealing features, metrics at the population, assemblage, and community levels may offer less power to detect effects of environmental degradation than individual-level measures (Underwood & Peterson 1988; Jones et al. 1991; Osenberg et al. 1994). The statistical power of an index depends on the relationship between the magnitude of the effect and background variation. In aquatic ecosystems, the density and composition of benthic animal assemblages are notoriously variable (Thrush et al. 1994; Sandin & Johnson 2000; Hewitt et al. 2001); therefore, both large effect sizes and abundant replication may be required to detect significant patterns attributable to environmental changes. For instance, Osenberg et al. (1994) found that large effects of coastal pollution on marine invertebrate populations are less likely to be detected than smaller effects on individuals because population-level measures are more variable. Measures at the individual level are also likely to respond more rapidly than those at higher levels, offering opportunities for early detection of problems and interpretation of causal pathways.

Anthropogenic sedimentation resulting from watershed disturbance is a growing threat to aquatic ecosystems worldwide (Groombridge & Jenkins 1998). Sedimentation has a variety of strong, direct effects on aquatic animals (reviewed in Rogers 1990; Ryan 1991; Johnson et al. 1993), including mortality resulting from the loss of suitable habitat or obstruction of feeding and

respiration (e.g., Rabeni & Smale 1995; Runde & Helenthal 2000; Donohue & Irvine 2003). Sedimentation can also have a variety of indirect effects mediated by shifts in food sources or predators (e.g., Kerby & Kats 1998) or changes in ecosystem processes such as nutrient cycling and primary production (Reice & Wohlenberg 1993).

We studied the effects of sedimentation on littoral snails in Lake Tanganyika, East Africa. Previous surveys in this large tropical lake have suggested that anthropogenic sedimentation reduces the local diversity of fishes, ostracods, and molluscs (Cohen et al. 1993; Alin et al. 1999). Experiments show that inundation of rocky substrates with sandy sediments significantly decreases the abundance of many invertebrates and fishes (Donohue et al. 2003), and addition of sand to laboratory microcosms increases mortality of snails and ostracods (Donohue & Irvine 2003). These results suggest that habitat degradation through anthropogenic sedimentation is a major threat to the endemic snails of Lake Tanganyika.

To better understand the effects of sedimentation on these unique snails, we recorded assemblage-level and individual-level data at sediment-disturbed and reference sites. Comparisons of species richness, evenness, and density were used to examine the effects on the snail assemblage. We expected strong reductions in all three measures based on the surveys and experiments we reviewed (see previous citations). We used individual-level data to examine the effects of sedimentation on four major aspects of snail ecology: predation intensity, risk of parasitism, food quality, and life history. Predatory crabs are a major source of mortality for Tanganyikan snails (West et al. 1991; West & Cohen 1996), parasitic trematodes castrate their host snail, and food quality strongly affects snail growth and reproduction. Changes in each of these factors are known to affect snail life history (Dillon 1997). In addition to comparing the sensitivity of individual- and assemblage-level indices to sedimentation, we discuss the value of individual-level survey data for evaluating direct and indirect pathways by which habitat degradation affects aquatic animals.

Methods

Study System and Snail Fauna

Lake Tanganyika is the oldest (~12 million years old) and deepest (~1470 m) of the East African rift lakes. It is a global hotspot of freshwater fish and invertebrate diversity (Groombridge & Jenkins 1998), but only a small percentage of the shoreline is formally protected inside parks. Most species in the lake are found exclusively in the narrow littoral zone (Coulter 1991; Michel 1994), where sand, cobble, boulder, and bedrock substrates are interspersed along the shoreline on scales of 10–1000 m. Bottom composition is usually similar from 0–10 m depth, although rocks sometimes give way to sand below the wave zone (~4 m).

The shoreline is steeply sloped in most areas because of uplift along the fault zone in which the lake lies. Native vegetation protects undisturbed shoreline slopes from erosion, and clearing shoreline vegetation for agricultural and urban development leads to sedimentation and turbidity (Alin et al. 1999; Alin et al. 2002). At disturbed sites, sediment blankets most horizontal surfaces and is resuspended daily by wave action.

Snails are conspicuous on rock surfaces in the littoral zone. We focused on relatively large-bodied species (shell length > 10 mm) that dominate snail biomass and diversity (13 of ~17 rock-dwelling species at these sites), including members of five endemic genera: *Lavigeria*, *Reymondia*, *Spekia*, *Paramelania*, and *Vinundu* (Michel 2004). Individual sites were inhabited by 6 to 8 of the 13 species. Some species have specific depth preferences (e.g., <2 m or >6 m), whereas others occur throughout the upper 15 m. Taxonomies of *Lavigeria* and *Paramelania* are under revision, and we adopted the open nomenclature set forth in West et al. (2003) and Michel et al. (2004).

These snail species are found on the lateral and upward surfaces of large rocks throughout the day and night, and usually move <60 cm/day (E. M., P. B. M., & J. Chan, unpublished data). They are algivores (Michel 2000), forming part of a diverse herbivore guild that includes many invertebrates and fishes. Previous research has identified predation by crabs as a major source of snail mortality in this system (West et al. 1991; West & Cohen 1996), but the prevalence of parasitism has not been studied previously.

Study Sites

Sediment-disturbed and reference sites were selected for comparison in a single-time, impact-reference framework (sensu Wiens & Parker 1995) because data for before and after comparisons are not available. In this approach, the effect of sedimentation on a focal variable is inferred from the statistical significance of the difference between sediment-disturbed and reference sites relative to the vari-

ance among sites within each category. We incorporated additional information such as water depth or shell size into analyses where appropriate, but the effect of survey year was not tested because the data from our two surveys were not combined.

We conducted surveys at six rocky littoral sites near Kigoma, Tanzania. Sediment-disturbed and reference sites were paired by proximity (<5 km): two sites were immediately south of Kigoma Bay, two were immediately north of Kigoma Bay, and two sites were ~35 km north of Kigoma near Gombe Stream National Park. The northernmost and southernmost pairs of sites were studied in 1998, but logistical constraints required studying the four southern sites in 2001. The substrate at each site was composed of cobbles, bedrock, and boulders sloping downward at 15–30° relative to horizontal.

Three sites (Mwamgongo, “Hilltop,” and Kalalangabo) were categorized as sediment-disturbed based on visible sediment accumulation in the littoral zone and exposure of the terrestrial soil surface. Mwamgongo (4°36'34" S, 29°38'34" E) is a large village located just north of Gombe Stream National Park, and its shoreline has been cleared and farmed for decades. The Hilltop site (4°53'15" S, 29°36'50" E) lies below a hotel on a bluff and experienced sedimentation during 3 years of continuous construction before our study began. Kalalangabo (4°50'10" S, 29°36'30" E, also called Mwamahunga Beach) is immediately north of a village, where the steep shoreline has been cleared and farmed throughout the study period.

We chose the three reference sites (Mitumba, “Jakobson’s Beach,” and “Euphorbia”) based on the absence of sediment on littoral rocks and the presence of relatively natural shoreline vegetation. Mitumba (4°38'04" S, 29°37'57" E) is protected within Gombe Stream National Park, and sediment cores show that it has experienced much less sedimentation than the nearby disturbed site at Mwamgongo since at least 1880 (Alin et al. 2002). Jakobson’s Beach (4°54'53" S, 29°35'53" E) is a private reserve with woodland covering the shoreline. Euphorbia (4°50'56" S, 29°36'30" E) is a 200-m woodland patch flanked by grass-covered agricultural fields that lay fallow for several years before and during the study period.

To validate disturbance categorizations and assess food availability for snails, we quantified sediment mass and periphyton biomass on eight large, flat cobbles (at 2 m depth) at the four southern study sites during August 2001 (Table 1). A snorkeler sealed a plastic cap over the center of each cobble to protect the overlying materials within a fixed area. Cobbles were carried to shore, and all material surrounding the cap was removed with a wire brush and discarded. From the area protected by the cap, we removed loose material (hereafter referred to as nonattached) with water from a squirt bottle and attached material with a wire brush. We collected two subsamples of each type on precombusted glass-fiber filters

Table 1. Materials on rocks 2 m deep at sediment-disturbed (S) and reference (R) sites.^a

| Site | Nonattached ^b | | | Attached ^c | | Total ^d | |
|----------------------------|---------------------------------|--|---------------------------------|--|---------------------------------|-----------------------|--|
| | dry mass (g/m ²) | chl a ^e (mg/m ²) | dry mass (g/m ²) | chl a ^e (mg/m ²) | dry mass (g/m ²) | organic% ^f | chl a ^e (mg/m ²) |
| Hilltop (S) | 218 (68) | 9.1 (0.1) | 76 (17) | 37.6 (6.3) | 295 (80) | 26 (4) | 46.7 (6.7) |
| Kalalangabo (S) | 648 (200) | 11.5 (3.2) | 70 (19) | 32.1 (4.7) | 719 (211) | 8 (1) | 46.6 (4.3) |
| Mwamgongo (S) ^g | — | — | — | — | 659 | 11 | 29.6 |
| Jakobsen's Beach (R) | 5 (1) | 1.4 (0.2) | 25 (3) | 14.9 (1.8) | 30 (4) | 63 (3) | 16.3 (1.9) |
| Euphorbia (R) | 32 (8) | 1.3 (0.4) | 24 (4) | 8.7 (1.5) | 57 (11) | 54 (10) | 10.0 (1.8) |
| Mitumba (R) ^g | — | — | — | — | 297 | 12 | 5.6 |

^aMeans (SE) are provided for each site (n = 8 rocks in most cases).

^bMaterial dislodged from rock surface with water from a squirt bottle.

^cMaterial that remained attached to rock surface during squirting and that was removed with a brush.

^dSum of nonattached and attached materials.

^eChlorophyll a concentration, as measured by spectrophotometer with an acidification step.

^fLoss of dry mass on ignition at 500° C for 3 hours.

^gData from O'Reilly (2001).

(Gelman A/E, Ann Arbor, Michigan). One subsample was dried to a constant mass (60° C, 48 hours), weighed, combusted (500° C, 3 hours), and reweighed to determine organic content (Sutherland 1998). The second subsample was extracted for 24 hours in 90% ethanol and analyzed for chlorophyll *a* with a spectrophotometer (including an acidification step; Nusch 1980). We used similar data from O'Reilly (2001) for the two northernmost study sites (Table 1).

Snail Surveys

We surveyed snail assemblages at two disturbed (Hilltop and Mwamgongo) and two reference (Jakobsen's Beach and Mitumba) sites during June–July 1998. Four depths (1, 2, 5, and 10 m) were studied to ensure that all large species were included. At each depth, divers established five replicate 4-m² quadrats (2 × 2 m) on large, upward-facing bedrock and boulder substrates separated by more than 5 m. Flexible, weighted lines allowed quadrats to adjust to the contours of the substrate, and only the upper surfaces of rocks were sampled in order to standardize the surface area and microhabitats studied. Extremely high snail densities at Hilltop required reducing some quadrats to 1 m² because of constraints on SCUBA time.

Snorkelers or divers collected every snail visible in each quadrat. We restricted analyses to individuals with shell length > 10 mm because preliminary work indicated that divers were unable to consistently recover smaller individuals from the sediment layer at disturbed sites. This size restriction may have excluded a few species from our survey; however, these species represent a trivial component of snail biomass and including them would have increased sampling error unacceptably.

Snails were brought back to the laboratory alive for species identification and processing. Species richness, evenness, and total snail density were calculated for each site and depth combination. Shell dimensions, brooding

status for viviparous *Lavigeria* species, number of shell scars, and presence of endoparasitic trematodes were recorded for all individuals up to a maximum of 30 individuals per species per quadrat. Shell scars from failed predation attempts are widely used as an index of predation pressure (Vermeij 1987; Leighton 2002), and they were clearly visible as jagged irregularities cutting across growth lines in the shells. To determine the presence of parasites, we crushed the gonad between glass plates and examined the material under a dissecting microscope for cercaria, redia, or sporocysts. Infection was recorded as present or absent for each individual snail, and cercaria morphotype was recorded, although taxonomic identification was not possible.

To assess effects of sedimentation on snail feeding, we collected snails at two sediment-disturbed (Hilltop and Kalalangabo) and two reference sites (Jakobsen's Beach and Euphorbia) during August 2001. We used the mass and organic content of feces as indices of food quality, with the expectation that consumption of inorganic sediments of low nutritional value would enhance fecal mass and decrease organic content. Sixty individuals from each of two to three species were collected at a depth of 2 m along 20 m of shoreline at each site. We cleaned each shell with a wire brush, and placed groups of 10 conspecifics together in clean containers (0.6 L). Containers had a mesh cover to prevent escape and were submerged together in a bath of aerated lake water. Snails were incubated for 16 hours to allow complete gut clearance, after which fecal matter was collected on filters and measured for organic content as described earlier.

Statistical Analyses

Because of the high variation in snail densities per quadrat in the 1998 survey, we pooled snails within each site-depth combination in our analysis of species richness and evenness. The total number of individuals collected

at each site and depth combination still varied widely (ranging from 62 to 1279), so species richness was rarified. Hurlbert's probability of an interspecific encounter (PIE), which describes the probability that two individuals drawn randomly from a pooled sample are different species, was used as an index of evenness in pooled samples. We calculated means and 95% confidence intervals for both indices with EcoSim (Gotelli & Entsminger 2001), based on 1000 random samples of 62 individuals for each site and depth combination. Evaluations of statistical significance were based on the confidence intervals.

We used partially nested, mixed-model analysis of variance (ANOVA) to evaluate the main and interactive effects of disturbance, site, and depth on snail density. Disturbance and depth were fixed factors, and site was a random factor nested within disturbance. Densities were log transformed before analysis.

L. nassa was the only species that was abundant at all sites and at most depths in the 1998 survey, so we selected it for comparisons of shell scarring and parasitism among sites. We used logistic regression models to estimate the effects of disturbance, depth, and shell length on the probability of having a scarred shell or being parasitized. Shell lengths were centered about the mean value for the entire data set. Due to the absence of *L. nassa* 1 m deep at one site, only data from 2, 5, and 10 m depths could be analyzed. We included interaction terms in preliminary models but eliminated them when they were not significant ($p > 0.1$). To clarify patterns of parasitism, we used chi-square tests to supplement the logistic regression model.

We compared the distributions of *L. nassa* shell lengths in 1998 among sites using Kolmogorov-Smirnov two-sample tests (hereafter referred to as K-S tests). We pooled data across depths for each site (range 64–182 snails) and made separate comparisons for brooding females and all *L. nassa*. We also compared sizes of conspecific snails among sites in the 2001 survey with K-S tests (60 snails per species per site).

We compared the masses of organic and inorganic material in snail feces among sites for each species. Preliminary models indicated a strong positive relationship between fecal mass and snail tissue mass (dry mass estimated from shell lengths with allometric equations with $R^2 = 0.82$ – 0.97 ; E. M., unpublished data), so we standardized for differences among sites in snail sizes by dividing fecal dry mass by estimated snail tissue mass. Standardized masses of organic and inorganic fecal matter were log transformed and compared among sites for each species with multivariate analysis of variance (MANOVA). Significant differences were further investigated using separate ANOVAs for organic and inorganic fecal matter.

We used Proc GLM in SAS version 8 (SAS Institute, Cary, North Carolina) to analyze all ANOVA models, with Tukey's honestly significantly different (HSD) adjustments for multiple comparisons to maintain alpha at

0.05. Data met statistical assumptions after transformation, with the exception of heteroscedasticity of snail densities in the 1998 survey. Logistic regression was performed with Proc GENMOD in SAS. We conducted K-S and chi-square tests in SYSTAT version 10 (Systat Software, Richmond, California), and we adjusted significance tests for multiple comparisons with the Bonferroni method (critical alpha = 0.008).

Results

Disturbance Categorizations and Food Availability

More material was found on rock surfaces at sediment-disturbed sites than at reference sites, but a lower proportion of this material was organic (Table 1). An exception to this pattern was the Mitumba reference site, where carbonates or sand on rocks increased the mass of material and decreased its organic content (O'Reilly 2001). Concentrations of chlorophyll *a* and organic material also were highest at disturbed sites (Table 1), and there was a positive relationship between these variables ($R^2 = 0.322$, $p = 0.022$, $n = 16$). Thus, rock surfaces at disturbed sites offered more algal food resources than at reference sites, but these resources were diluted within a large amount of inorganic material.

Snail Surveys

Thirteen snail species were collected in the 1998 survey (Table 2), all of which are endemic to Lake Tanganyika. Pooled across depths, sediment-disturbed sites hosted seven (Hilltop) and six (Mwamgongo) species compared with seven (Jakobsen's Beach) and eight (Mitumba) species at reference sites. Sedimentation was not associated with a change in the mean or variance of rarified species richness, and there were no overall differences among sites (Fig. 1). The lowest estimates of species richness for particular depths were from disturbed sites, but there was considerable variation among depths within every site. Two species (*L. grandis* and *Paramelania* sp. C) were found at both reference sites but at neither disturbed site, but the reverse was not true for any species (Table 2).

Sedimentation was associated with reduced evenness of snail species representation, as measured by Hurlbert's PIE, at some depths (Fig. 1). There were no consistent differences at 1 or 5 m, but evenness was significantly higher at reference sites at 2 and 10 m. No general patterns of evenness were seen with depth, but variation within and among depths was higher at sediment-disturbed sites.

Mean snail densities ranged from 3 to 64 individuals/m² (Fig. 1). Densities did not differ significantly between sediment-disturbed and reference site categories ($F_{1,2} = 0.05$, $p = 0.845$); however, differences between sites within categories were significant ($F_{2,6} = 8.54$,

Table 2. Distribution of snail species across depths (1, 2, 5, and 10 m) at sediment-disturbed and reference sites in 1998.*

| Species | Sediment disturbed | | | | | | | | Reference | | | | | | | |
|---------------------------|--------------------|-----|-----|------|---------|-----|------|------|------------------|-----|-----|------|---------|-----|-----|------|
| | Mwamgongo | | | | Hilltop | | | | Jakobsen's Beach | | | | Mitumba | | | |
| | 1 m | 2 m | 5 m | 10 m | 1 m | 2 m | 5 m | 10 m | 1 m | 2 m | 5 m | 10 m | 1 m | 2 m | 5 m | 10 m |
| <i>Lavigeria nassa</i> | 1.0 | 3.4 | 4.1 | 0.1 | 8.8 | 5.5 | 1.6 | 2.0 | — | 0.2 | 1.7 | 1.6 | 0.2 | 1.0 | 4.0 | 2.2 |
| <i>Lavigeria grandis</i> | — | — | — | — | — | — | — | — | 1.7 | 1.4 | 0.2 | 0.1 | 4.0 | 5.0 | 1.3 | — |
| <i>Lavigeria coronata</i> | — | — | — | — | — | — | — | — | 0.1 | 1.0 | 3.0 | 0.8 | — | — | — | — |
| <i>Lavigeria</i> sp. B | — | — | — | — | — | — | — | — | — | — | — | — | 0.1 | 2.5 | — | — |
| <i>Lavigeria</i> sp. J | — | — | — | — | 2.6 | 5.4 | 62.2 | 25.0 | — | — | — | — | — | — | — | — |
| <i>Lavigeria</i> sp. M | — | — | — | — | 0.3 | 0.6 | — | — | — | — | — | — | — | — | — | — |
| <i>Lavigeria</i> sp. X | — | — | — | — | — | 0.1 | 0.3 | — | — | — | — | — | — | — | — | — |
| <i>Paramelania damoni</i> | — | — | 0.1 | — | — | — | — | — | — | — | — | — | — | — | — | 0.2 |
| <i>Paramelania</i> sp. C | — | — | — | — | — | — | — | — | — | — | — | 0.1 | — | — | 0.1 | — |
| <i>Reymondia borei</i> | 3.5 | 0.1 | — | 0.1 | 0.2 | — | — | — | 4.4 | 0.8 | 0.1 | 0.1 | 9.0 | 1.8 | — | — |
| <i>Spekia zonata</i> | 4.5 | 0.2 | — | — | — | 0.1 | — | — | 0.7 | — | — | — | 4.6 | 0.1 | — | — |
| <i>Vinundu guillemei</i> | — | — | — | 0.8 | — | — | — | — | — | — | — | 1.3 | — | — | — | — |
| <i>Vinundu westae</i> | — | — | 3.4 | 2.2 | — | — | — | 0.2 | — | — | — | — | — | 0.2 | 2.4 | 1.1 |

*Mean densities (individuals per square meter) are shown for four depths per site ($n = 5$ quadrats).

$p = 0.018$). This effect was driven by large differences between the two sediment-disturbed sites ($p < 0.001$); reference sites were not significantly different ($p = 0.179$). Snail densities did not differ consistently among depths ($F_{3,6} = 1.60$, $p = 0.286$), and there were no significant interactions between depth and sedimentation or sites. The variance in density within and among depths at a given site, however, was higher at sediment-disturbed sites.

L. nassa had 0–5 shell scars each, and 13–69% of individuals at each site had at least one scar (Fig. 2). The probability of bearing scars was significantly lower at disturbed sites ($z = -2.48$, $p < 0.02$), and small snails were less likely to have scars than larger snails ($z = 4.47$, $p < 0.001$). There were no significant effects of depth or interactions among predictors.

The incidence of parasitism was 3–7% at sediment-disturbed sites and 19–22% at reference sites (Fig. 2). Seven morphotypes of trematode cercaria were found in *L. nassa*, all of which completely destroyed the gonad. There was no clear pattern of morphotype diversity relative to sedimentation; five and two types were recorded from the disturbed Hilltop and Mwamgongo sites, respectively, compared with three at each reference site.

The statistical patterns of parasite frequency were complex. The logistic regression model indicated that the probability of being parasitized increased with depth ($z = 3.75$, $p < 0.001$) and shell size ($z = 25.98$, $p < 0.001$) but was unaffected by sediment disturbance ($z = -0.50$, $p = 0.614$). Significant interactions of disturbance with depth ($z = 2.92$, $p < 0.004$) and size ($z = -6.98$, $p < 0.001$), however, prevented interpretation of the main effects. Instead, we pooled snails across depths and compared the total proportion of adult-sized *L. nassa* that were parasitized at each site ($n = 48$ –182 individuals per site). The size threshold was based on the smallest brooding female observed at each site, thereby accounting for

differences among sites in size at maturity. The proportion of adult-sized *L. nassa* castrated by parasites was significantly higher at reference sites (Jakobsen's Beach, 25%; Mitumba, 22%) than at disturbed sites (Hilltop, 7%; Mwamgongo, 3%) but similar within disturbance categories (chi-square tests: all comparisons $p < 0.008$ between categories, $p > 0.4$ within categories).

Snail fecal mass and organic content differed significantly between sediment-disturbed and reference sites (Table 3). The size-standardized mass of organic matter in feces was generally higher at disturbed sites, but this pattern varied across species and sites. There was significantly more (3–11 \times) inorganic matter in feces of all species at disturbed sites; thus, the total mass of feces produced by snails of all sizes and species was higher at disturbed sites. Organic matter made up 46–66% of fecal mass at reference sites but only 22–39% at sediment-disturbed sites.

L. nassa were smaller at disturbed sites than at reference sites in 1998 based on comparisons of both brooding females and entire populations (K-S tests, $p < 0.003$; Fig. 3). Size distributions at the two reference sites were statistically indistinguishable, but *L. nassa* were larger at Mwamgongo than at Hilltop ($p < 0.003$). Females at the reference sites did not initiate reproduction until they reached a much larger size than their counterparts at disturbed sites. Shell sizes in the 2001 survey were also shifted downward at disturbed sites for *L. nassa* and *L. grandis* but not for *R. borei* (Table 3).

Discussion

Our surveys indicated that anthropogenic sedimentation has many strong effects on littoral snails in Lake Tanganyika. Assemblage-level measures of impact, however,

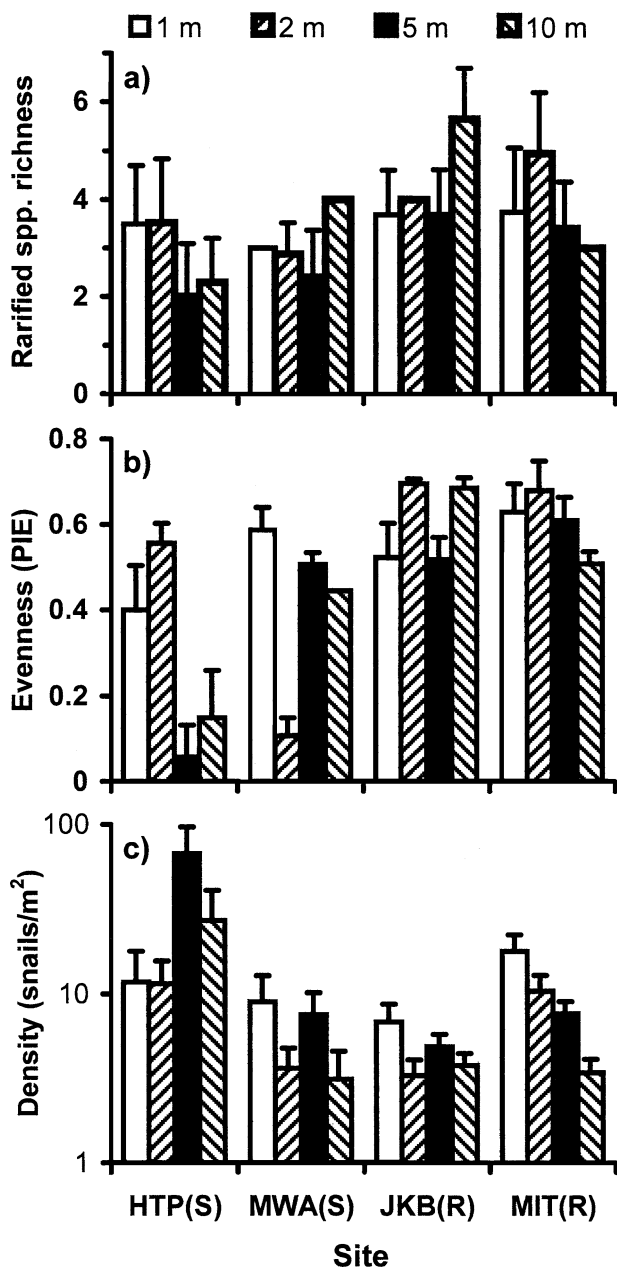


Figure 1. (a) Rarified species richness, (b) evenness, and (c) density of snails at sediment-disturbed (S) and reference (R) sites. Mean rarified species richness and evenness, measured as Hurlbert's probability of an interspecific encounter (PIE), are calculated from 1000 simulated samples of 62 individuals from each site and depth combination. Error bars are 95% confidence intervals from simulations. Mean (+SE) snail density is based on five quadrats at each site and depth combination. Site abbreviations: HTP, Hilltop; MWA, Mwangongo; JKB, Jakobsen's Beach; and MIT, Mitumba.

suggested few differences between sediment-disturbed and reference sites (Fig. 1). Rarified species richness was highly variable both within and among sites in 1998 and offered little evidence that sedimentation reduces snail

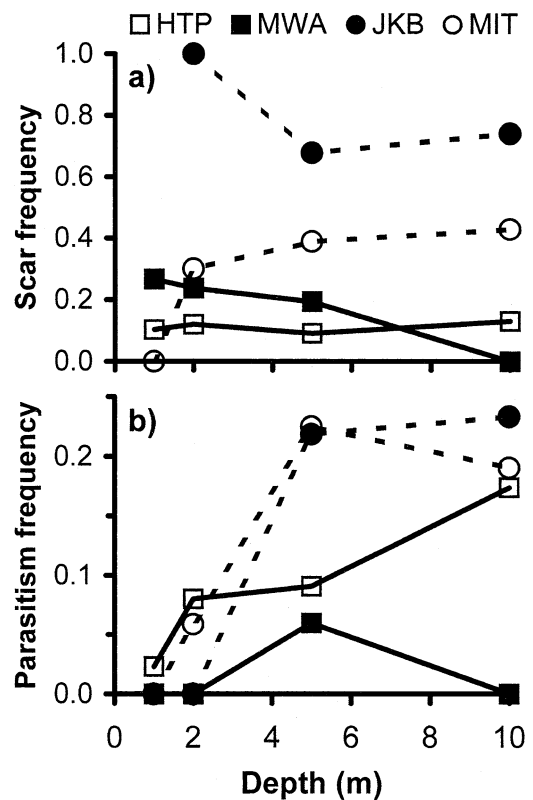


Figure 2. Frequency of (a) shell scarring and (b) parasitism by trematodes of *Lavigeria nassa*. Sediment-disturbed sites are indicated by solid lines and square markers; reference sites are indicated by dashed lines and circles. Proportions represent data from only two snails at the following site and depth combinations: Jakobsen's Beach (JKB), 2 m; Mitumba (MIT), 1 m; and Mwangongo (MWA), 10 m. No individuals were found at 1 m at JKB. At least 10 snails were evaluated for all other site and depth combinations.

diversity. Evenness at depths of 2 and 10 m was lower at disturbed sites but comparable to reference sites at depths of 1 and 5 m. Snail densities did not differ consistently among sites or depths, although variance was highest at disturbed sites. Together, these measures suggest only weak effects of sedimentation on the composition and abundance of the snail assemblage.

We expected to find much stronger assemblage-level effects of sedimentation based on the survey results of Alin et al. (1999) and experimental tests (Donohue & Irvine 2003; Donohue et al. 2003). Several differences between these studies and ours may be important. Alin et al. (1999) surveyed three sites representing increasing degrees of sedimentation but observed significant differences between only the most and least disturbed sites. These sites were separated by >70 km, resulting in unintentional sampling of two biogeographic regions of *Lavigeria* endemism (Michel et al. 2004). Our analysis of nearby replicate sites within disturbance categories

Table 3. Size and fecal statistics for snails from reference (R) and sediment-disturbed (S) sites in 2001.^a

| Species | Site | Shell length (mm) ^b | Fecal mass (mg feces/g snail) ^c | | Fecal organic content (%) ^d |
|--------------------------|----------------------|--------------------------------|--|---------------|--|
| | | | organic | inorganic | |
| <i>Lavigeria nassa</i> | Euphorbia (R) | 17.4–24.4a | 18.9 (1.1)a | 23.2 (3.3)a | 46 |
| | Jakobsen's Beach (R) | 13.1–25.8a | 24.5 (1.8)a | 20.4 (2.3)a | 55 |
| | Kalalangabo 1 (S) | 15.0–23.4b | 22.6 (1.0)a | 65.6 (4.3)b | 26 |
| | Hilltop (S) | 9.5–15.1c | 65.6 (5.6)b | 150.2 (11.6)c | 30 |
| <i>Lavigeria grandis</i> | Euphorbia (R) | 20.3–27.8a | 16.4 (0.9)a | 13.1 (2.2)a | 57 |
| | Kalalangabo 1 (S) | 16.8–24.4b | 39.9 (2.3)b | 145.2 (9.9)b | 22 |
| <i>Lavigeria</i> sp. M | Hilltop (S) | 7.5–10.6 | 141.9 (28.8) | 218.1 (36.8) | 39 |
| <i>Reymondia borei</i> | Euphorbia (R) | 6.4–14.2a | 53.3 (3.3)a | 69.9 (12.4)a | 46 |
| | Jakobsen's Beach (R) | 9.7–14.5a | 61.6 (3.9)ab | 35.3 (6.2)a | 66 |
| | Kalalangabo 1 (S) | 8.9–14.2a | 78.4 (10.7)b | 222.6 (39.2)b | 27 |
| <i>Spekia zonata</i> | Jakobsen's Beach (R) | 6.9–13.5 | 29.2 (2.4) | 17.8 (2.6) | 63 |

^aLetters (a, b) indicate significant differences among populations within species.

^bRange among 60 individuals per population.

^cMean (and SE) calculated following standardization for estimated snail tissue dry mass (n = 6).

^dPercentage of fecal dry mass loss on ignition at 500° C for 3 hours.

offers a more stringent test of the assemblage-level consequences of sedimentation, and it minimizes the risk of confounding biogeographic patterns with sedimentation effects. In addition, Alin et al. (1999) collected snails and bivalves of all species and sizes, so it is possible they included species that differ in sensitivity to sedimentation from those we studied. Finally, their sites in northern Lake Tanganyika may have been subjected to a longer period of sedimentation than our Hilltop and Kalalangabo sites, although Mwamgongo has experienced elevated rates of sedimentation since at least 1880 (Alin et al. 2002).

Results of experimental sediment manipulations also predicted strong assemblage-level effects. Inundating a rock substrate with sand resulted in high mortality of *R. borei* in a laboratory experiment (Donohue & Irvine 2003). In the field, blanketing the substrate with sandy sediments resulted in reduced densities of the dominant snail species (*L. grandis*) and a nonsignificant loss of snail diversity (Donohue et al. 2003). These results suggest that snail densities should be lowest at sediment-disturbed sites. In fact, the highest snail densities were recorded at disturbed sites in both our survey (Fig. 1) and that of Alin et al. (1999). Both the type of sediment (sand) and sediment mass (80 kg/m²) used in these experiments differed from the thin layer (<1 kg/m²) of organic-rich silt present at disturbed sites in northeastern Lake Tanganyika, and it remains to be seen whether the experimental results can predict field patterns elsewhere.

In contrast to the lack of clear effects of sedimentation at the assemblage level, individual-level measures indicated pervasive changes in snail ecology. Sediment-disturbed sites were characterized by 20–82% lower frequencies of shell scarring in *L. nassa* (Fig. 2), suggesting partial release from a major source of mortality. Our analyses indicated that this was not an artifact of smaller shell size at disturbed sites. Reduced predation is likely

to have important demographic consequences for these snails and to relax a key evolutionary pressure (West et al. 1991; West & Cohen 1996). Crabs are the only predators capable of scarring large *L. nassa*, but the effects of sedimentation on the density and foraging of these predators are unknown.

Parasitism of *L. nassa* by trematode flatworms was also significantly less common at sediment-disturbed sites (Fig. 2). Trematodes castrate their host, creating a subpopulation of snails that compete with nonparasitized conspecifics but cannot reproduce (Dillon 1997). The frequency of parasitism of adult-sized *L. nassa* at reference

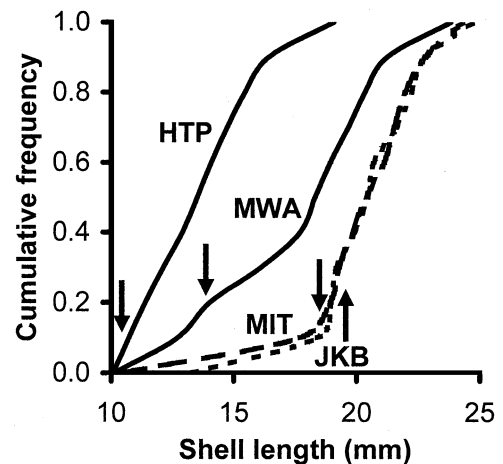


Figure 3. Cumulative frequency distribution of shell lengths of *Lavigeria nassa* in 1998. Sediment-disturbed sites are indicated by solid lines; reference sites are indicated by dashed lines. Arrows indicate the size of the smallest brooding female recovered at each site. Site abbreviations: HTP, Hilltop; MWA, Mwamgongo; JKB, Jakobsen's Beach; and MIT, Mitumba.

sites (22–25%) was unusually high for freshwater snails (typically 0–10%; Dillon 1997), and more recent surveys indicate that these frequencies have been maintained at both reference and disturbed sites (K. Faloon et al., unpublished data). Anthropogenic disturbance can influence the prevalence of parasitism in snails (Lafferty & Kuris 1999), but the pathway by which *L. nassa* are affected is unknown. Infection requires that a snail encounter a trematode egg or miracidia, and sedimentation could reduce the viability of these trematode life stages, the probability of contact with a snail, or the abundance of definitive hosts delivering new eggs to the substrate (e.g., Lafferty 1993b). In any case, the low frequency of parasitism at disturbed sites could affect *L. nassa* population dynamics by increasing the proportion of adults capable of reproduction (e.g., Lafferty 1993a).

Fecal data indicate that snails at disturbed sites ingested more material than conspecifics at reference sites (Table 3). As predicted, inorganic material accounted for most of the difference in fecal mass, suggesting that the quality of ingested material was reduced at disturbed sites even though standing stocks of algae and organic matter were higher (Table 1). The fact that snail feces had higher organic content than bulk material collected from rock surfaces at disturbed sites shows that they fed selectively but ingested large amounts of inorganic material nonetheless (e.g., Connor & Edgar 1982). In contrast, snail feces at reference sites had lower organic content than material on rocks, as expected following the digestion of organic material. Food quantity is positively related to growth and reproductive output in snails (Dillon 1997), yet the lack of a snail density response to higher algal biomass at disturbed sites suggests that even increased ingestion and selective feeding are insufficient to overcome the reduced food quality associated with sedimentation (Broekhuizen et al. 2001).

Finally, sedimentation was associated with a striking downward shift in size distributions of most species (Table 3). Corresponding shifts in the size distribution of brooding *L. nassa* and size at first reproduction indicate that this pattern was neither a sampling artifact nor a reflection of parasitic gigantism (Fig. 3). These life history shifts are unlikely to have been mediated by reduced mortality from predators and parasites at disturbed sites because size at maturity is inversely related to risk of predation and parasitism in snails (e.g., Hershey 1990; Lafferty 1993b; Jokela et al. 1999). It is more likely that low growth resulting from poor food quality at disturbed sites resulted in maturation at a fixed age but at smaller sizes than at reference sites (e.g., Brown 1985), but direct measurements of growth rates are required to test this hypothesis. Regardless of its causes, the small size of snails at disturbed sites is expected to reduce the per capita fecundity of oviparous species (i.e., *Reymondia*, *Spekia*, *Paramelania*, *Vinundu*; Dillon 1997). *Lavigeria*, however, are viviparous and their brood sizes are inde-

pendent of female size (E. M. & I. Kingma, unpublished data).

Taken together, the patterns of predation, parasitism, food quality, and life history we documented provide strong evidence that sedimentation alters the ecology of the endemic snails of Lake Tanganyika. We are unsure why ramifications of these changes were not apparent at the assemblage level, although it is tempting to speculate that the benefits of partial release from parasitism and predation offset the costs of poor food quality at disturbed sites (Snyder & Ives 2001). The lack of assemblage-level response to sedimentation cannot be construed as a general lack of effect, and our results support the continued need to protect these snails from habitat degradation.

Although the Tanganyikan fauna is distinctive in many aspects of its ecology and evolution (West et al. 1991; Michel 2000), we expect that sedimentation will affect snail feeding, predation, and parasitism in other aquatic ecosystems. Our results are most relevant to lakes and coastal marine areas. Regardless of ecosystem type, the demographic implications of shifts in interspecific interactions caused by habitat degradation will depend on the ecology of the particular species involved and are likely to defy generalization.

Comparing Assemblage- and Individual-Level Measures

Many authors have suggested that assemblage- and population-level measures offer low power to detect the effects of environmental degradation because they are inherently noisy (Underwood & Peterson 1988; Jones et al. 1991; Osenberg et al. 1994; Byers & Goldwasser 2001). The diversity, evenness, and density of benthic organisms are notoriously variable (e.g., Thrush et al. 1994; Sandin & Johnson 2000; Hewitt et al. 2001), and our surveys support this generalization (Fig. 1). Our results, however, do not fit the scenario outlined by Osenberg et al. (1994) and Johnson (1998), in which fairly large effects of disturbance were overwhelmed by high background variation. In our study, differences in assemblage-level patterns between the two disturbance categories were generally small and inconsistent, with the exception of evenness at 2 and 10 m (Fig. 1). Comparing these small effects to the substantial variation between sites within disturbance categories suggests that even a survey of many more sites would be unlikely to detect an influence of sedimentation on snail richness, evenness, and abundance.

In contrast, individual-level data consistently indicated strong effects of sedimentation on snails. The superior sensitivity of individual-level measures may result from integration of fewer influences than population-, assemblage-, or community-level metrics. For example, declines in population size or species diversity of long-lived organisms often lag behind their causes because effects on individuals propagate upward slowly (Tilman

et al. 1994). Individual-level data such as life-history characteristics or food quality will usually change more rapidly (e.g., Byers & Goldwasser 2001). This responsiveness could allow conservation biologists and managers to identify threats before population declines and extinctions occur, thereby facilitating prevention and remediation.

Individual-level data can also offer insight into the pathways through which disturbance affects organisms. The distinction between direct and indirect effects has clarified controls on patterns and processes in aquatic ecosystems (Kerfoot & Sih 1987; Wootton 1994; Menge 1995), and our surveys show that disturbance can have strong indirect effects as well as the direct ones that are usually assumed to have primacy (Vitt et al. 1998; Golet et al. 2002). For instance, the observed reductions in scarring and parasitism at disturbed sites constitute indirect effects of sedimentation on snails. Although manipulative experiments are required to separate the relative magnitude of direct and indirect effects, individual-level survey data often may be useful for testing whether interspecific interactions have been affected by disturbance. In this study, documenting these pathways enriched our understanding of the effects of sedimentation on snails and revealed impacts on other trophic levels.

Our results demonstrate the utility of incorporating individual-level measures into environmental impact surveys alongside assemblage-level measures. Although assemblage-level measures are needed to address patterns of diversity and abundance, the greater sensitivity of individual-level metrics may offer earlier detection of effects and facilitate interpretation of causal pathways. In our surveys, quantifying patterns at both levels revealed a variety of previously unrecognized effects of sedimentation on snails, including indirect effects through predators and parasites.

Acknowledgments

This work was financed by the Nyanza Project (National Science Foundation [NSF] grant ATM9619458), the United Nations Global Environmental Facility (Lake Tanganyika Biodiversity Project), and an NSF fellowship to P.B.M. Logistical assistance was provided by the Tanzanian Fisheries Research Institute, Kigoma, and especially D. Chitamwebwa. J. Jokela and M. Rigby trained us in parasitology. C. O'Reilly provided sedimentation data, and S. Nshinyabakobeje and F. Vermeulen furnished statistical advice. K. Hora, G. Kazumbe, C. Menone, M. Phifer, C. Solomon, and A. Socci assisted in the field. We thank S. Alin, H. Beasley, D. Cleary, A. Flecker and the Flecker lab group, M. Genner, H. Lenihan, J. Melack, C. O'Reilly, J. Todd, and anonymous reviewers for comments on the manuscript. This is contribution 154 of the International Decade of East African Lakes.

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