

# **Trematode parasite prevalence in *Lavigeria*: The effects of sedimentation, depth, size and species**

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## **Introduction**

The deposition of anthropogenic sediment in aquatic areas has profound effects on the ecology of aquatic littoral communities. The effects of sedimentation in the rocky littoral of Lake Tanganyika have been documented for a variety of species (Cohen et al. 1993). Alin et al. (1999) found that sedimentation affects the ecology of fish, snails and ostracods as well as species density, abundance and richness. Further investigation by McIntyre et al. (submitted) delved deeper into the direct and indirect effects of sedimentation on the community, finding that direct and indirect effects may offset each other in their effects on populations. My study aimed to take a closer look at the prevalence of parasitism in *Lavigeria* gastropods, its relationship to sedimentation, and how parasite prevalence changed between species. Based on the trends seen in McIntyre (submitted), one would predict lower parasite prevalence in sedimented sites.

The life cycle of a trematode parasite may vary with the type of parasite, but generally starts as excretion of eggs from the final host in urine or feces. Eggs hatch into miracidia larvae once they hit the water and find a snail host. Once inside the host the gonad is targeted and redia are produced, which make parasite cercaria larvae. Cercaria larvae hatch out of the snail and have three days to find its final host before it dies (Roberts). An example of a final host would be a fish, mammal or bird.

Trematode parasites castrate their snail hosts, creating a situation in which individuals are using community resources, but are reproductively dead. The interaction between trematode parasites and their snail hosts has been likened to that of a predator-prey relationship because it ends the reproductive capacity of that individual. However it is different because the host may be able to adjust its' life history before it is fully incapacitated reproductively (Krist and Lively 1998). The infection of snails by parasites is thus an important influence on the evolution of snail life history parameters, especially on timing because it results in a genetic death for the host (Ruiz 1990; Jokela and Lively 1995).

The benefit of being a parasite is that it can suck energy from its host without much cost once it finds the host. However, it is important to keep the host alive, or else the parasite loses its home and source of energy. Targeting infection to a host's non-maintenance function is a common infection strategy. Adult molluscs devote a large proportion of their energy to reproduction, so the gonad is an obvious target for trematode parasites because it is not essential to sustaining the life of the host (Jokela et al 1993).

The effect of parasites on life history of snails has been studied a number of different systems for many different kinds of parasites. Parasites have been found to either stunt or enhance growth in their snail hosts, which may depend on the age of infection (Krist and Lively 1998). In the case of increased growth, the theory is that because the snail can not use its energy for reproduction, it is diverted to growth, leading to gigantism (Williams and Brailsford 1998). However, if the castration is not complete, the snail may divert more energy to reproduction to get a higher return, causing it to grow to smaller size (Williams and Brailsford 1998).

In general, there is a positive relationship between parasitism, age and size. Larger, older individuals are more likely to be parasitized because they have been around longer and there is a greater probability that they will encounter parasites (Krist and Lively 1998). This relationship would indicate that as snails have co-evolved with parasites over time they would tend to have a reduced age and size at first reproduction, especially when the probability of infection is high (Ruiz 1990; Jokela and Lively 1995). Prevalence in *L. nassa* appears to be abnormally high (Dillon 2000), indicating evolutionary selection pressure by trematode parasites in Lake Tanganyika. Total parasitism is also variable with depth, site and habitat type, indicating

that selection by parasites varies with spatial location and habitat, potentially yielding local differences in selection pressure on life history traits.

Sedimentation can lead to a loss of heterogeneity in habitat, altering the infection of snails by parasites. This is supported by McIntyre et al. (submitted); sites impacted by sedimentation had lower parasite prevalence as compared to pristine sites and that infection increased with depth. The sizes of local populations of the same species also varied between sites, potentially due to lower food quality. However, parasitism has been shown previously to alter growth (Williams and Brailsford 1998) and can not be discounted as an important factor shaping the evolution of life history parameters of snail species. In order to assess how important parasitism is in shaping the evolution of life history characteristics of the gastropod species of Lake Tanganyika, a good measure of prevalence must be obtained. This study aimed to measure prevalence of *Lavigeria* species and how prevalence changes temporally, with sediment impacts, depth and across species.

### Methods

Snail collection took place at six sites along the eastern shore of Lake Tanganyika near Kigoma, Tanzania. The substrate was composed of large boulders and rocks with varied degrees of sedimentation depending on location and the condition of the surrounding shoreline. Sediment impacted and reference sites were paired in close proximity, no more than 5 km from each other to minimize regional differences.

Sediment impacted sites were chosen based on previous studies conducted along the shoreline that tested sediment effects (McIntyre et al. submitted; Rivers 2001). A site was considered impacted based on the accumulation of sediment on the bottom substrate and erosion exposure of the surrounding terrestrial landscape. "Hilltop" is a site located at the foot of a cliff on which a hotel stands, the slopes of which experienced a large amount of erosion during and after construction. Kalalangabo is a fishing village located north of Kigoma; the surrounding hillside is farmed for cassava and has steep landslides. Mwamgongo is a large village located north of Gombe Stream National Park, has been extensively farmed and seen explosive population growth in the last 10 years. Reference sites were located in areas with relatively "natural" terrestrial vegetation without presence of exogenous sediment on aquatic substrate. "Jakobsen's" is located in a private reserve, Kalalangabo 3 is surrounded by vegetated hillside and Mitumba is located inside Gombe Stream National Park. For ease of analysis paired sites were divided into North, Central and South locations. Mitumba and Mwamgongo comprised the North sites, Kalalangabo 2 and 3 are Central sites and Jakobsen's and Hilltop are South sites (see biology map).

*Lavigeria nassa* was chosen as a focal species for study between impacted and non-impacted sites based on a preliminary study that indicated its presence at adequate densities at 5m at the chosen sites (McIntyre et al., submitted). Densities of *L. nassa* were based on 10 1m<sup>2</sup> rope quadrats placed on chosen boulder tops, for homogeneity of substrate, at each site at 5m depth. Individuals of larger size class were chosen, spanning a 10mm size range, to encompass individuals on the verge and at reproductive maturity. One hundred-plus *L. nassa* were collected by divers along the 5 m contour over a distance of 50+ m. Specimens were brought to the lab, where they were maintained for up to 2 days prior to processing. At the Jakobsen's Beach site, I collected three *Lavigeria* species (*L. grandis*, *L. nassa*, *L. coronata*) for comparison of trematode infection frequencies. The former two species were also sampled at Kalalangabo 3; *L. coronata* was not collected from that site due to concerns about the impact of destructive sampling on that population.

Shell height, lip thickness and sex data was recorded for every individual. The shell was cracked using a hammer and the gonad was dissected, sex determined and squashed between two glass plates. The presence or absence of trematode cercaria in the gonadal tissue was evaluated and the trematode morphotype recorded. Further identification of trematode species was not possible, however, specimens have been preserved for later investigation. All parasites found were classified as digenian trematodes, probably belonging to the superfamily Strigeoidea (Frandsen and Christensen 1984; Roberts).

Parasite "prevalence" was chosen as a comparative measure based on the definition in Bush et al. 1997. Prevalence is "the number of hosts infected with one or more individuals of a parasite species divided by the number of host examined for that parasite species" (Bush et al. 1997). Data analysis was conducted using SAS version 8. Logistic regressions were performed on the data and standard error was calculated

for parasite prevalence based on Lively and Jokela (1996) using the equation  $SE=(p*(1-p)/N)^{1/2}$  where  $p$ =prevalence  $N$ =sample size. Population level differences in snail size distributions were accounted for by scaling the size of each individual to the largest individual in the sample, which was called "relative snail size" for purposes of analysis. Data used in depth comparison was collected as defined in Chan 2002 and in the multi-year comparison from McIntyre et al. (submitted).

## Results

Prevalence of parasite infection varied as a function of both sedimentation and latitude. For each pair of sites, reference sites had a higher parasite prevalence than sedimented sites (Fig. 1  $p=0.08$ ; Table 1). Paired site location resulted in significantly different prevalence of parasites between South sites and both North and Central sites,  $p=0.031$  and  $0.0003$  respectively (Fig. 1; Table 1). There was also a significant positive relationship between size and parasite prevalence ( $p<0.0001$ ; Table 1). There was no interaction between relative shell size, latitude and site ( $p>0.2$ ), so it was removed from the final model.

In the inter-species comparison at the reference sites (non-sediment impacted), *L. nassa* had a significantly higher prevalence rate than *L. grandis* or *L. coronata* (Fig. 2,  $p<0.0001$ ; Table 2). There was no significant difference between *L. grandis* and *L. coronata* (Fig. 2,  $p=0.97$ ; Table 2). Jakobsens beach (JKB) had a higher parasite prevalence for both species than Kalalangabo (KLG3) ( $p=0.0003$ ; Table 2) and the lack of interaction between species and site indicates that the interspecific difference was uniform across sites (Fig. 2,  $p=0.72$ ; Table 2). Four morphotypes of parasite were found in *L. nassa*, two in *L. grandis* and one in *L. coronata*. They all appeared to be different types, suggesting that parasite infection was species specific. Density varied across site and species, however no pattern emerged relating parasite prevalence and density (Fig. 3).

Size varied by approximately 10mm for each site and was generally similar for paired sites. The exception was Jakobssen's and Hilltop in which the sedimented site (HTP) had smaller sized individuals than the reference site (JKB) (Table 3). In initial comparisons of depth effects on parasite prevalence, the trend is toward increased parasitism at deeper depth in all three species (Fig. 4). However, the methods used for the 3m and 5m collections were not the same, resulting in high variation in 3m data and no ability to test significance of this trend. In comparing the two years of parasite data, similar trends in parasite prevalence were found, although the numbers were varied due to differing sampling methods. In both the 1998 and 2002 data set parasites increased with a decrease in sedimentation across both paired sites (Fig. 5).

## Discussion

This study shows variation in parasite prevalence relative to size, species, ontogeny and sedimentation. Our results show that there was higher parasite prevalence in reference sites as compared with sedimented sites for a given location (Fig. 1). Potential explanations for this trend are that 1) sediments prevent trematode miracidia from finding snail hosts either by decreasing survival or movement 2) sediments cause a decrease the supply of eggs by decreasing the abundance of the definitive host in the area or that 3) parasitized individuals are less likely to survive under sediment conditions (McIntyre et al. submitted). The mode of parasite transmission (active or passive) to a snail host is dependent on parasite life history, which is unknown for these particular parasites. However, micro predators are more commonly found in sandy environments, causing parasite larvae to potentially face higher predation pressure in sedimented areas (McIntyre et al. submitted) or simply face more challenging swimming and sensory conditions in turbid water. Secondly, a decrease in diversity and abundance of potential definitive hosts such as fish have been documented at sedimented sites (Cohen et al. 1993; Alin et al. 1999), which could lead to a smaller supply of eggs and larvae. Spatial location and habitat is very important to parasite prevalence and distribution (Jokela and Lively 1995) which also may explain the variation we see between prevalence and location of pairs of sites (Fig. 1). Differences in spatial patterns would also lead to differences in selection pressure on life history trait evolution. Lastly, the combination of parasitism, which reduces survival (Jokela and Lively), and sedimentation, which potentially leads to reduced growth and poor nutrition (Rivers 2001, McIntyre et al. submitted), could cause a higher mortality in parasitized individuals, leading to a lower prevalence.

In the comparison of parasite prevalence across species, *L. nassa* had a significantly higher percentage than the other species (Fig. 2; Table 1). This could be related to distribution, as *L. nassa* is widely distributed

throughout the shoreline in abundant densities, while *L. grandis* is less dense at 5m and *L. coronata* is found only at two known sites (Fig 3.). Because parasite prevalence is abnormally high in *L. nassa* (Dillon 2000) selection pressure of parasites is higher on *L. nassa* than on the other species. In combination with other factors such as predation and food, this could contribute to size differences between sites on the lake as seen in McIntyre et al (submitted).

General depth and temporal patterns were also evident. Parasitism appears to increase with depth for both *L. nassa* and *L. grandis* (Fig. 4), which agrees with findings in the literature (Lively and Jokela 1996; McIntyre et al. submitted). A potential explanation for this trend is that physical factors such as wave action and turbidity are decreased at deeper depth, making it more probable to find a host. Parasite behavior also may favor infection at depth because they often passively fall in the water column until disturbed (Roberts), or definitive hosts may be located at deeper depths. Snail behavior may also change because of parasite infection, leading to changes in location more suitable to contact with the parasites final host (Jokela and Lively 1995).

Parasite prevalence also seems to be temporally stable across a number of years, as does the trend of lower parasitism at sedimented sites (Fig. 5; McIntyre et al submitted). Relative to the available literature on parasite prevalence in molluscs, the parasite prevalence found for *L. nassa* is extremely high, while prevalence in *L. grandis* and *L. coronata* is comparable to rates found in snail populations in other systems(Dillon 2000). This extreme rate, in combination with the temporal stability of this trend, indicates intense selection pressure by parasites on *L. nassa*. Because parasites can cause changes in life history parameters such as size and reproduction (Krist and Lively 1998), parasitism is a potentially significant factor affecting snail species evolution in Lake Tanganyika.

Future investigations could focus further on the parasite prevalence differences between different species. In particular a comparison between species W and *L. nassa* might be especially interesting. Species W has a very similar appearance to *L. nassa* but secretes a mucous. Given the comparatively high prevalence of parasites in *L. nassa*, it would be interesting to see if a mucous makes a difference. Another interesting study would be parasite prevalence in soft substrate species such as Sp. AA, Sp. X and *Paramelania* to see if naturally occurring sedimentation affects parasitism as opposed to the anthropocentric sedimentation examined in this study. Further investigation into parasitism prevalence of different species may be able to elucidate some of the variation seen in species and localized population life history parameters in Lake Tanganyika.

Parameter	DF	Chi Square	P value
Sedimentation	1	3.12	0.08
Latitude Central and South	1	13.41	0.0003**
Latitude North and South	1	4.66	0.031*
Sediment *Central and South	1	0.02	0.88NS
Sediment *North and South	1	.37	0.54NS
Relative shell size	1	19.18	<0.0001**

**Table 1.** Effect of sedimentation on *L. nassa* across paired sites. South included Jakobsen's (R) and Hilltop (S), Central includes Kalalangabo R and S and North includes Mitumba (R) and Mwamgongo (S). Significant p values are marked with \* and highly significant values are marked with \*\*.

Site	Comparison	DF	Chi Square	P value
JKB (South)	<i>L. nassa</i> , <i>L. grandis</i>	1	31.80	<0.0001**
JKB	<i>L. coronata</i> , <i>L. nassa</i>	1	43.10	<0.0001**
JKB	<i>L. coronata</i> , <i>L. grandis</i>	1	2.75	0.97NS
KLG 3(Central)	<i>L. nassa</i> , <i>L. grandis</i>	1	12.17	<0.0001**
JKB and KLG3	Site	1	12.99	0.0003*
JKB and KLG3	Site*Species	1	2.81	0.7202 NS

**Table 2.** Species and site comparison at the pristine sites for *L. nassa*, *L. grandis* and *L. coronata*. Significant p values are marked with \* and highly significant values are marked with \*\*.

Location	Site	Size range (mm)	Site	Size range (mm)
North	MBA (R)	13.49-24.51	MWG (S)	12.81-24.88
Central	KLG 3(R)	13.68-23.42	KLG 2 (S)	13.19-24.76
South	JKB (R)	13.52-24.99	HTP (S)	9.21-20.42

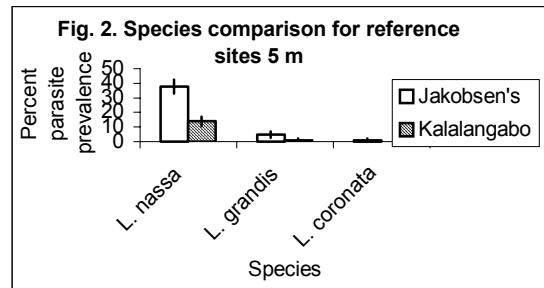
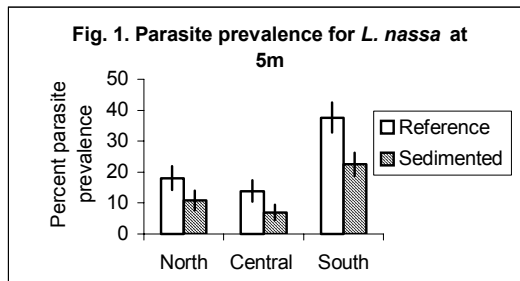
**Table 3.** Size comparison between sites. Size ranges were compiled based on sample size of approximately 100+ individuals for each site collected as stated in methods.

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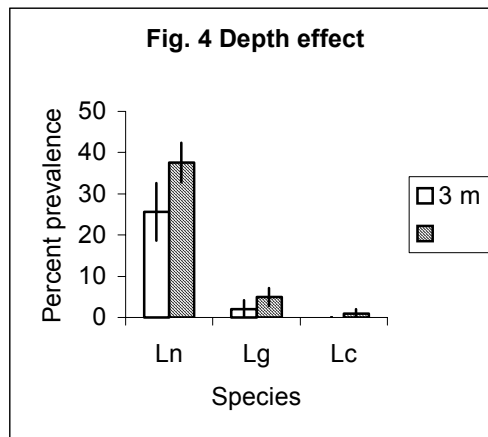
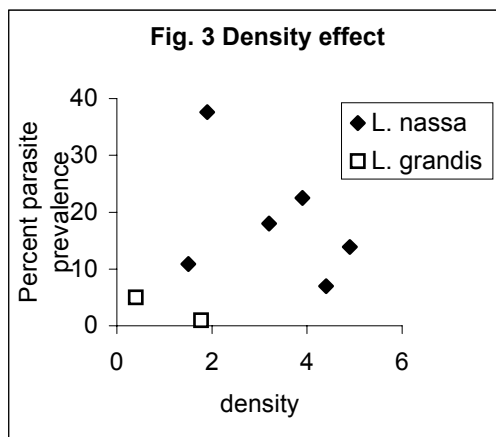
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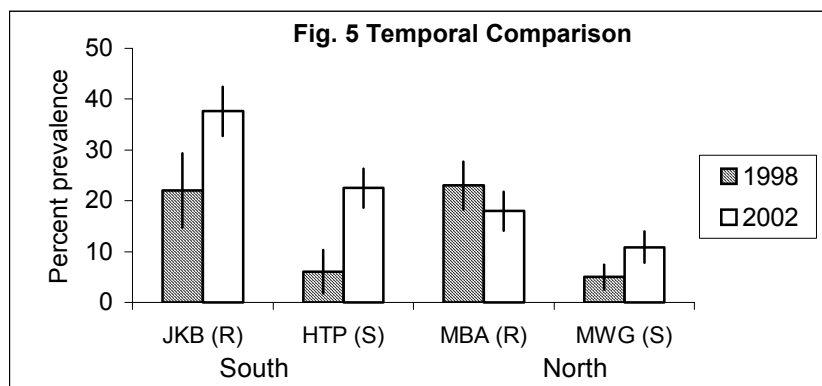
**Figure 1:** Parasite prevalence for *L. nassa* at 5m. Prevalence is the percentage of sampled individuals infected with trematode parasites. North, Central and South represent geographically paired sites of reference and sedimented areas as shown on the biology map and described in methods. (See table 1 for statistics.)

**Figure 2:** Species comparison for reference sites at 5m depth. *Lavigeria nassa*, *L. grandis* and *L. coronata* were sampled at two reference sites: Jakobsen's beach and Kalalangabo 3. See table 2 for statistics.



**Figure 3:** Density effect. Densities were measured for *L. nassa* and *L. grandis* and plotted against depth using parasite prevalence at each of the sites.

**Figure 4:** Depth effect. Parasite prevalence of each species was compared across depth using snails collected as detailed in Chan 2002.



**Figure 5:** Temporal comparison for *L. nassa*. Parasite prevalence in *L. nassa* was compared at 4 sites for 1998 and 2002. The same trends were evident, although hard number changed, potentially due to a difference in sampling methodology.