EFFECT OF NERITID SNAILS ON THE ABUNDANCE OF ALGAE AND PALAEMONID SHRIMP IN A NEOTROPICAL STREAM

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Abstract: In aquatic systems, grazing by herbivores may increase resource availability and structural heterogeneity. In the Rio Claro, Corcovado National Park, Costa Rica, we observed algal and neritid snail abundances, which we hypothesized were inversely related. Through field observations and manipulations, we tested for patterns of abundances and interactions among snails, algae, and palaemonid shrimp. We found that snail abundance was negatively related to algal cover and shrimp abundance. But there were no apparent negative interactions between shrimp and snails over a 24 h period. Snails were patchily distributed throughout the stream, but overdispersed within patches. We speculate that snail effects on resource availability and habitat structure could increase invertebrate abundance in general, as well as exerting positive effects on palaemonid shrimp.

Key Words: herbivory, structural heterogeneity, trophic dynamics, tropical streams

INTRODUCTION

Algal and invertebrate communities are closely coupled in aquatic systems (Poff and Nelson-Baker 1997). Periphyton cover of rocks may provide both food and habitat for invertebrate grazers, which in turn can influence abundance of algae. Invertebrate taxa may also interact directly or indirectly, e.g. by altering shared resources (Pennak 1953).

In the Rio Claro in Corcovado National Park, Costa Rica, there is spatial variation in both algal cover and invertebrate species composition, among nearby sections of the stream. We hypothesized that snail abundance would be negatively correlated with both algal cover and shrimp abundance. Snails are bulldozer grazers of algae (Sommer 2000). Shrimp, as omnivore grazers (Pennak 1953), may compete with snails for food or habitat. We also predicted that interactions with shrimp would reduce grazing by snails.

METHODS

We conducted three experiments on the Rio Claro, approximately 3 km upstream of its estuary near Sirena, Corcovado National Park, Costa Rica on 2-4 February 2005.

First, we measured snail and shrimp abundance and percent algal cover in 22 quadrats (1 m^2) along a 250 m stretch of the Rio Claro. Thirteen quadrats were selected at approximately 20 m intervals, An additional four were selected in a reach with low snail abundance, and five more were in a reach with particularly high snail abundance. To quantify patchiness on the scale of quadrats, we used a variance to mean ratio (VMR) applied to shrimp and snail abundances in the 13 quadrats dis-

tributed at 20 m intervals. A VMR equal to 1 indicates random dispersion, while a value › 1 indicates aggregation and a value ‹ 1 indicates hyperdispersion. We used JMP 5.0.1 to perform linear regressions of the relationships between shrimp abundance, snail abundance, and algal cover in the quadrats. All of our data except algal cover met the normality assumptions of the parametric tests performed. Neither log nor square root transformations were able to normalize percent algal cover.

Second, we tested for the effects of shrimp on snail grazing by excluding shrimp from cages, with three levels of snail abundance (0, 5, and 10 per cage). Thus, cages were exclosures for shrimp, but enclosures for snails. All cages, constructed from half-minnow traps with a diameter of 22 cm, were submerged in the Rio Claro at a site with 100% algal-covered rocks. We prepared two replicates of each snail abundance treatment; one was covered in mesh to prevent any shrimp from entering the cage, while the other was left open so shrimp could enter. After 24 h, we quantified percent algal cover in each cage. We ran a two-way ANOVA to compare the effect of snail abundance and shrimp presence/absence on change in percent algal cover, as well as the effect of shrimp on snail grazing.

Thirdly, we tested for effects of snail presence on shrimp abundance with a container experiment. Containers were plastic storage containers of two different sizes, 1.2 m^3 and 0.5 m^3. Only two of each size container were available, thus limiting the number of replicates. We put 20 shrimp in each large container and 5 shrimp in each small container, and then created a snail treatment by adding 20 and 5 snails, respectively, to one container of each size. We used different shrimp and snail abundances in the two different-sized containers to approximate equal organism:tank volume ratios in all of our enclosures. We measured shrimp abundance after 36 h, and used a one-way ANOVA to compare the abundance of shrimp in treatments with and without snails.

RESULTS

From our quadrat sampling, we found that snail abundance was inversely related to both shrimp abundance (r^2 = 0.41, df = 21, P = 0.0014; Fig. 1a) and algal cover (r^2 = 0.60, df = 21, P < 0.0001; Fig. 1b).

In our measure of snail and shrimp dispersion over 250 m of stream, we found that shrimp were slightly aggregated on a 1 m^2 scale (VMR = 1.53), while snails were more strongly aggregated (VMR = 6.96). Our 250 m transect included four distinct substrate types: pebble-dominated, directly upstream and downstream of a riffle; a sandy area; and an area dominated by cobbles. Within those substrate types, snails were generally overdispersed and shrimp were approximately randomly dispersed (Fig. 2).

In the algal grazer experiment with three levels of snail density, algal cover decreased with greater snail abundance (ANOVA, F = 48.44, df = 1, 2, P = 0.07; Fig. 3). Each snail treatment produced significantly different levels of algal abundance

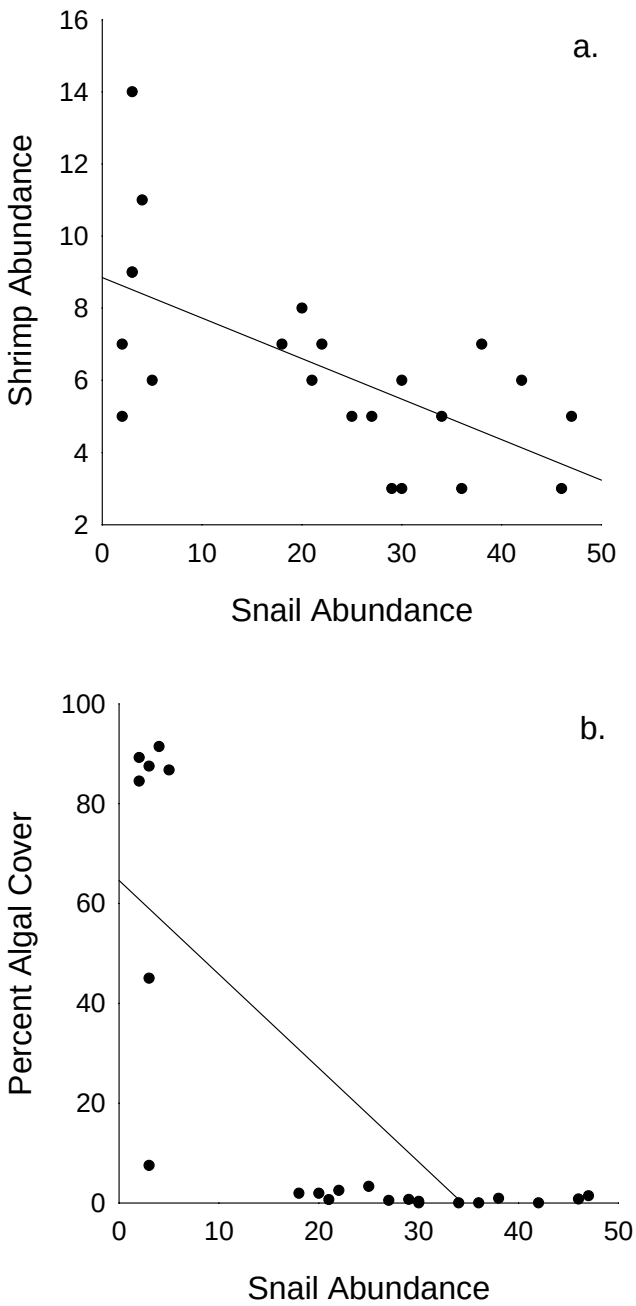

Figure 1. Negative relationship between snail and shrimp abundance (a, Number of Shrimp = 8.8 - 0.1 Number of Snails) and snails and percent algal cover (b, % Algae Cover = 64.6 - 1.9 Number of Snails) in 22 quadrats along a 250 m section of the Rio Claro, Corcovado National Park, Costa Rica.

(Tukey's HSD test, $\alpha = 0.05$). There was no effect of shrimp presence on change in algal cover (F = 0.07, df = 1, 2, P = 0.81).

In our third experiment, we found no change in shrimp abundance over time due to snail presence in our containers (ANOVA, F = 0.00, df = 1, 2, P = 1.00).

DISCUSSION

Our findings indicate that snail distribution may be a key factor in determining local algal abundance in the Rio Claro. Our quadrat sampling over 250 m showed a strong negative relationship between snail abundance and algal cover, and our enclosure experiments showed that increased snail density exerted additional grazing pressure on algae. Sommer (2000) found that snails, as bulldozer grazers, greatly decrease local spatial heterogeneity of microalgal biofilms by removing all algal cover in a patch over a short time period.

Snails were patchily distributed in the Rio Claro, but overdispersed within substrate types, which may be due to intraspecific competition in preferred patches. A possible explanation for the snail patchiness across the 250 m section of stream that we sampled is that juvenile snails may tend to compensate for downstream drift by migrating upstream in aggregated formations (Schneider 1986, 1993).

We found that snail abundance was inversely related to shrimp abundance in the stream. However, neither of our cage and container experiments, which manipulated snail and shrimp presence, revealed any negative interaction between snails and shrimp. This may be because the time

	Downstream		-250 m-		Upstream
Snail dispersion VMR	0.53		0.81	0.00	0.18
	Pebble 1	Riffle	Pebble 2	Sand	Cobble
Shrimp dispersion VMR	0.76		0.23	1.09	1.00

Figure 2. Snail and shrimp dispersion within four patches (Pebble 1, Pebble 2, Sand, Cobble) over 250 m of the Rio Claro, Corcovado National Park, C.R.

interval of our experiments was too short to observe the effects of any negative interaction between snails and shrimp, and/or due to inadequate replication. Further, different results would be obtained depending on how freely organisms were allowed to move in and out of the experimental units. It is also possible that the negative relationship between snail and shrimp abundance is a result of more complex trophic dynamics involving the changes in algal distribution caused by snail grazing. Previous stream studies have shown that a low level of snail grazing may actually increase abundance and diversity of other invertebrates by increasing algal cover heterogeneity, which in turn can provide more diverse food and habitat (Poff and Nelson-Baker 1997, Sommer 2000). This idea is consistent with our finding that shrimp were more abundant in areas of the stream with fewer snails and more algal cover, than in areas of high snail abundance and low algal cover. Although shrimp do not graze on the periphytic algae in our system, shrimp abundance is related to the abundance of other invertebrates, because shrimp scavenge on other invertebrate remains (Pennak 1953). Therefore, it is possible that at low snail densities, algae are abundant and the invertebrates that use those algae provide a food resource for the shrimp. Further research is needed to establish the links between snail grazing and invertebrate abundance, to determine the interactions between shrimp and snails, and to elucidate the causes of snail patchiness in the Rio

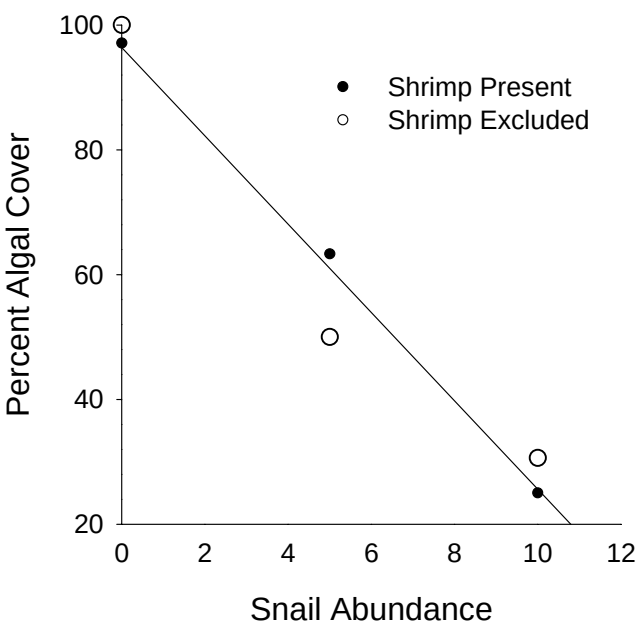

Figure 3. The negative effect of three snail abundance levels (0, 5, and 10 snails) on algal cover of rocks in exclosures submerged in the Rio Claro (% Algae Cover = 96.4 - 7.1 Snail Abundance, r2 = 0.97, df = 5, P = 0.0004). Shrimp presence had no effect on snail grazing.

Claro.

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