MACROBRACHIUM AS A POSSIBLE DETERMINANT OF *ASTYANAX FASCIATUS* DISTRIBUTION IN A NEOTROPICAL LOWLAND STREAM

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Abstract: The giant shrimp *Macrobrachium*, sp. is a possible nocturnal predator on the tetra *Astyanax fasciatus* and therefore may affect their spatial distribution within a stream. We observed the natural distributions of tetras during the day and night in a stream, and performed controlled manipulations to test for effects of shrimp on fish behavior. The horizontal and vertical distribution of tetras varied between day and night, but not as predicted under the hypothesis of shrimp avoidance. In an aquarium, tetras moved away from shrimp, clumping together at night and spreading apart during the day. Shrimp predation may be a factor influencing the spatial distribution of tetras on the Osa Peninsula, but other predators and food availability are probably also important.

Key words: Corcovado, giant shrimp, predation pressure, predator-prey interactions, tetra

INTRODUCTION

The tetra, *Astyanax fasciatus* (Characidae), and the giant shrimp, *Macrobrachium* sp. (Palaemonidae), co-exist in streams near Sirena Biological Station, Corcovado National Park, Costa Rica. The giant shrimp can prey on tetras in experimental enclosures (Brown et al. 2000); if this predation also occurs in nature, it could affect the activity patterns and distribution of tetras. If so, night would pose increased predation pressure on tetras because shrimp are nocturnal. Thus, tetras might be expected to congregate higher in the water column and away from the edges of the stream (to separate themselves from the benthic shrimp). We tested these predictions with surveys of tetra location during the day and night. Also, tetras might be expected to perceive the presence of shrimp and adjust their position accordingly. We tested this by recording fish locations within an aquarium (with and without shrimp).

METHODS

On 5 February 2004 we observed the abundance and distribution of tetra fish in the low-order stream, Quebrada Cameronal, at Corcovado National Park, Costa Rica. We keyed fish to genus and consulted Winemiller (1983) to determine tetra species; *A. fasciatus* is the only species in this genus listed at Corcovado. At each of five pools we set up a 50 cm wide cross-section of the stream; this cross-section was then divided into grids of 40 cm long rectangles. Before each observation, we stood still in front of the cross-section for 2 min to acclimate fish to our presence. We then counted the number of tetras and giant shrimp in each grid area at the bottom, middle, and surface of the stream (each equal to one-third of the vertical profile). We also noted any feeding maneuvers by the tetras or the presence of other fish species within the sampling grid. This was repeated at each pool twice during the morning and twice again that night. For each sample grid, we also measured the depth, temperature, and percent area of the benthos covered by organic matter. At each pool, we measured the surface flow (as the velocity of a floating object). For our analyses, we classified each rectangle as edge or mid-stream and calculated the density of fish within each rectangle using estimates of volume based on depth at the center of each rectangle. Tetra abundances and tetra densities per m^3 were log transformed (x + 1) to improve normality. We

analyzed tetra abundance with an ANOVA model that included pool, depth, time of day, and depth x time of day. We analyzed tetra density with an equivalent model, except with horizontal location (edge or middle) substituted for depth.

On 6 February 2004 we performed an experiment to measure the effect of shrimp presence on tetra distribution during the day and night. We set up a 61 x 41 x 30 cm tank of stream water and added ten individually distinctive tetras. After 15 min, we observed the three-dimensional position of each fish within the tank from a corner defined as the origin (depth of each fish was estimated as 0 - 10, 11 - 20, or 21 - 30 cm). We then added a shrimp (~ 15 cm long) enclosed in a clear, breathable bag in one corner (the origin), waited 15 min, and observed the fish locations again. We repeated this procedure once during the day and once at night, both with and without shrimp. Nine of the ten tetras were used for all four trials (one individual died between day and night trials). The water in the tank was changed after shrimp trials.

We generated a null model of tetra distribution within the tank using randomly generated coordinates. The test statistic was average distance to the origin (in three-dimensional space) of ten fish. We calculated a frequency distribution of 999 averages (based upon the null hypothesis of random dispersion) against which to compare the actual average distance observed in each of our four trials. Actual fish locations were judged to be nonrandom if their average distance was greater that 95% of the randomly generated frequency distribution.

We also calculated inter-fish distances for each pair of ten tetras in each treatment and compared them with a two-way ANOVA (day versus night and shrimp versus no shrimp). This analysis assumes independence of observations, although our experimental design did not strictly satisfy this condition (only 10 individuals were observed but 45 inter-fish distances were calculated). Consequently, the associated P-values were treated as approximate.

RESULTS

In our field observations, tetra abundance (fish per 0.2 m^2) was greater during the day than at night ($F_{1,59} = 13.49$, $P = 0.0006$) and greatest at mid-depths in the water column ($F_{2,59} = 21.64$, $P < 0.0001$; Fig. 1). There was no significant interaction between time of day and depth ($F_{2,59} = 2.37$, $P = 0.10$). Tetras were also more abundant in edge areas than mid-stream ($F_{1,119} = 26.11$, $P < 0.0001$); there was no interaction between horizontal location and time of day ($F_{1,119} = 2.77$, $P = 0.10$; Fig. 2). There were also main effects of pool on tetra abundance ($F_{4,59} = 24.93$, $P < 0.0001$) and tetra density ($F_{4,119} = 4.93$, $P = 0.001$). Surface flow was negligible in all study pools and temperature was almost invariate across time, locations, and depth (range = 26.4 - 27.6 °C), so we eliminated abiotic factors from our analyses.

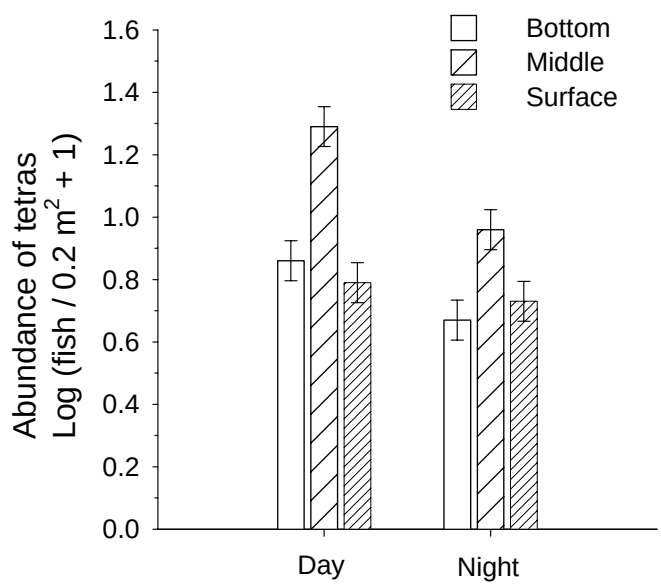

Figure 1. Abundance of *A. fasciatus* (means ± SE) during the day and night in the bottom, middle, and top of the water column of Quebrada Cameronal in Corcovado National Park, Costa Rica (n = 10 observations for each bar).

Fish density at day and night was also unrelated to percent organic matter in each rectangle (r = 0.17, P = 0.23 and r = 0.10, P = 0.55, respectively).

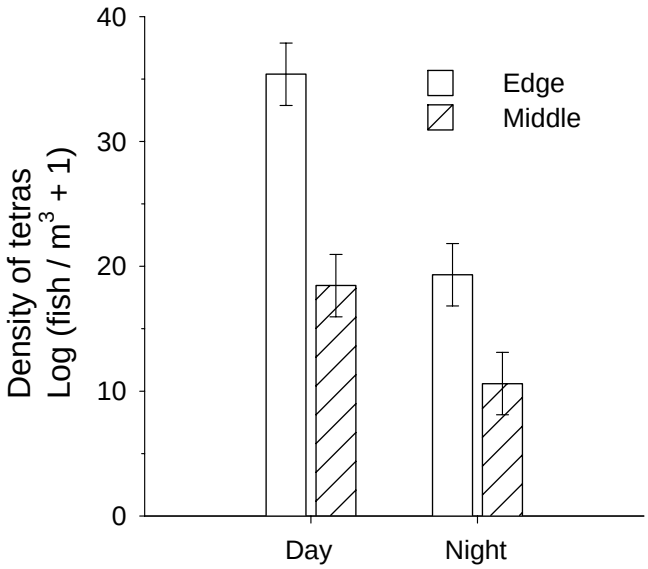

Figure 2. Density of *A. fasciatus* (means ± SE) during the day and night at the edge and mid-stream locations of Quebrada Cameronal in Corcovado National Park, Costa Rica (n = 30 observations for each bar).

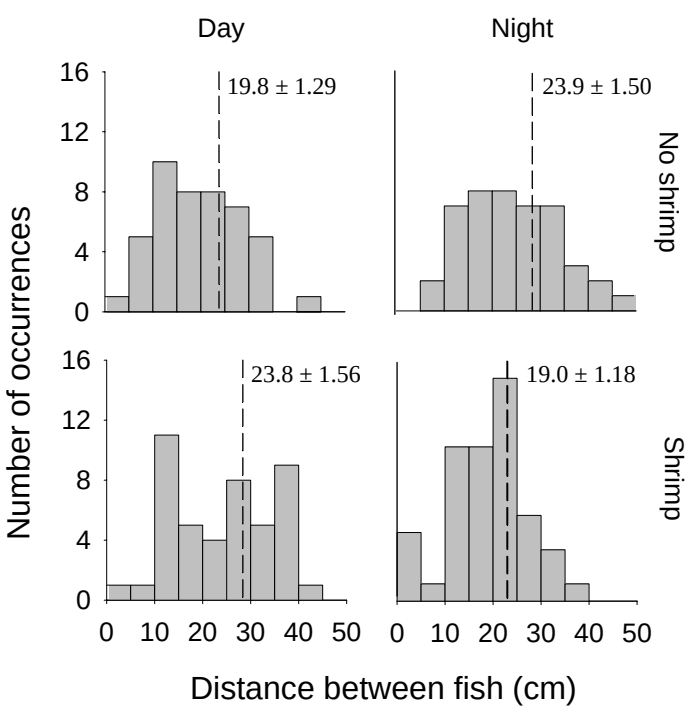

Figure 3. Frequency distribution of distances between fish in day trial (left) and night trials (right) with shrimp (bottom) and without shrimp (top). Means ± SE reported for each distribution. Vertical lines represent mean values.

We observed 15 events of tetra feeding maneuvers at the bottom of the stream and seven at the surface. Within our plots, we saw no shrimp during the day but 12 shrimp at night.

In our experimental manipulations, tetra in control treatments distributed themselves randomly with respect to the origin (mean distances for day and night = 47.6 and 46.2 cm versus expected distance under null model of 44.2 cm; P > 0.23 for both night and day). In the presence of shrimp, however, tetra tended to avoid predation by distributing themselves farther from the origin: 50.2 cm during the day (P = 0.11) and 55.3 cm at night (P = 0.01). The addition of a shrimp caused fish to shift farther apart from each other during the day and closer together at night. Main effects of shrimp and time of day were non-significant ($F_{1,179}$ = 0.076, P = 0.78); effect of shrimp x time of day was significant ($F_{1,179}$ = 10.31, P = 0.002; Fig. 3).

Discussion

There was a change in tetra abundance between day and night, but not in the directions that were predicted. Higher fish density in edge rather than midstream habitat suggests that there are greater benefits or fewer costs for tetras near the banks. Food availability may be higher or predation risk may be lower away from deep midstream areas. Tetras may be most abundant at intermediate depths because they are both surface and bottom feeders, and this position provides access to both food sources. However, we found no relationship between percent cover of organic matter and tetra position within a cross-section, so benthic food resources alone cannot fully explain distribution of tetras. Negligible variation in surface flow and temperature suggest that abiotic factors are not responsible for the observed distributions.

Our manipulative experiment demon-

strated that tetras respond to shrimp as though they are potential predators. Fish moved away from the shrimp during both day and night. At night, fish also became more clumped (smaller inter-fish distance) in the presence of shrimp, perhaps because being in a group reduces the chance that any one individual will be killed during a predation event. The fact that fish spread out in the presence of shrimp during the day may not be biologically relevant because shrimp seem to be inactive during the day, but it does demonstrate that reduced inter-fish distance was not a necessary consequence of avoiding the shrimp in the corner. It is also possible that during the day, grouping increases the risk from day-active predators which may be attracted to aggregations of tetras.

Our experimental manipulations show that in a controlled setting, shrimp do affect the spatial distribution of the fish. Our stream observations, however, indicate that shrimp predation is only one factor determining where fish are located in streams. The distribution of fish is likely a balance between foraging benefits and predator avoidance. Additionally, predation pressure in a stream may come from all directions (e.g. kingfishers and herons from above, caimans and piscivorous fish from below), further influencing the spatial distribution of tetras. Future studies should examine foraging behavior and food resource location as well as the effects of other predators as factors affecting *A. fasciatus* distribution.

LITERATURE CITED

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