TEMPORAL PARTITIONING OF FEEDING IN TROPICAL MARSH FISH OF LAGUNA PALO VERDE

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Abstract: Several fish species co-occur in the tropical marsh system of Laguna Palo Verde. We hypothesized that these fish temporally partition feeding activity in the relatively small areas of open water. We tested this hypothesis by comparing fish abundances and gut contents at dawn and in the afternoon. All the fish showed the same pattern of high feeding and abundance in the afternoon, and low feeding and abundance at dawn. This pattern is probably due to the co-incindence of lower predation pressures and higher feeding efficacy in the afternoon.

Key words: Cichlidae, competitive exclusion, niche

INTRODUCTION

According to the competitive exclusion principle, coexistence of species requires a differentiation of realized niches, a "partitioning of resources" (Begon et al. 1990). In lentic aquatic systems, resources can be partitioned in at least three ways: spatially, as fish occupy their preferred habitats; by prey type, as fish choose different food items; and temporally, as fish feed at different times.

Several fish species coexist in Laguna Palo Verde, a large wetland in Palo Verde National Park, in Guanacaste province of northwest Cost Rica. These species include *Herotilapia multispinosa, Achrocentrus nigrofasciatus, Astatheros longimanus, Parachromis managuensis,* and *Oreochromis nilotica* (Cichlidae), *Astyanax aeneus* (Characidae) and *Poecilia gillii* (Poecillidae) (Vargas et al. 2002, unpub. manuscript).

These fish may partition prey types (Bussing 1998). For example, *P. managuensis* possesses large sharp teeth adapted to a partly piscivorous diet, while *H. multispinosa*, a species of similar size, has tricuspid teeth better suited for consuming algae and detritus (Bussing 1998).

Fish may partition the marsh spatially among preferred microhabitats, as has been shown for the marsh's zooplankton (Poulin et al. 1998). Alternatively, open water, which is uncommon in the marsh relative to the area covered by aquatic vegetation, may be preferred by fish species because of the potential for efficient foraging (Bussing 1998). In this case, temporal partitioning of feeding (e.g. day vs. night) could help minimize interspecific competition among fish.

We tested for temporal partitioning in open water areas by measuring diel patterns in the abundance and feeding intensities of the fish species that co-occur within this habitat.

METHODS

We took three samples with a seine net at mid-afternoon (1500) and three in the morning (0600). We restricted our measurements to *H. multispinosa, A. longimanus, P. managuensis, A. aeneus* and *P. gillii*. Samples were taken in open water areas, all in a long strip that was 4 - 6 m wide. This strip of open water was bordered on both sides by a mix of floating vegetation and thick patches of *Thalia geniculata* and *Typha dominguensis*. Two of us dragged the net for approximately 8 m, while two associates attempted to drive fish into the net from the opposite direction. Fish were identified, counted, and released in the field. To evaluate feeding intensity, we dissected 17 fish that died during the netting (four to eight per species); we visu-

ally inspected the contents of each fish's gut, and assigned a gut fullness ranking of zero, one, two, or three. *P. gillii* was not evaluated for gut fullness because of its small size.

We used 2 - way ANOVAs to test for the effect of time and species on abundance (catch size) and gut fullness. Catch sizes were log transformed to correct for heteroscedasticity.

RESULTS

Mean catch sizes were significantly larger in the afternoon ($F_{1,16}$ = 15.58, P = 0.0012; Fig. 1). Catch sizes differed significantly among the four species ($F_{3,16}$ = 6.33, P = 0.005): *P. gillii* was the most abundant, followed by *A. aeneus*, *H. multispinosa*, and *P. managuensis* (mean catch size = 28.5, 12.7, 5.3, 0.7). There was no significant interaction between sampling time and species in catch size ($F_{3,16}$ = 0.76, P = 0.53).

Fish guts were generally empty in the morning and relatively full in the afternoon. Mean gut fullness index was significantly higher in the afternoon ($F_{1,11}$ = 24.30, P = 0.0005; Fig. 2). Gut fullness did not differ among species ($F_{2,11}$ = 0.49, P = 0.62), nor was there a significant interaction between time of day and species ($F_{2,11}$ = 0.93, P = 0.42).

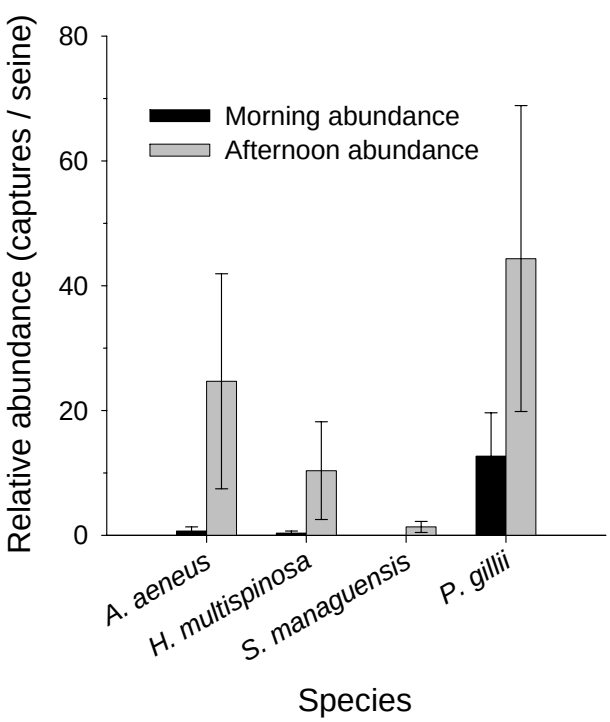

Figure 1. Relative abundances (± SE) in morning and afternoon of four species of fish in Palo Verde Marsh.

DISCUSSION

Our data indicate temporal trends in fish feeding and activity, but argue against temporal partitioning of feeding activity among species. Higher captures and higher gut fullness in the afternoon indicate that these fish feed on a similar schedule, in the same environment.

Visual feeding and predator avoidance are two likely explanations for this pattern. These fish are all visual feeders and may rely on direct sunlight to locate prey in the turbid marsh water. Major predators of fish in the marsh include crocodilians, fishing bats, and birds (potentially, herons, egrets, storks, osprey,

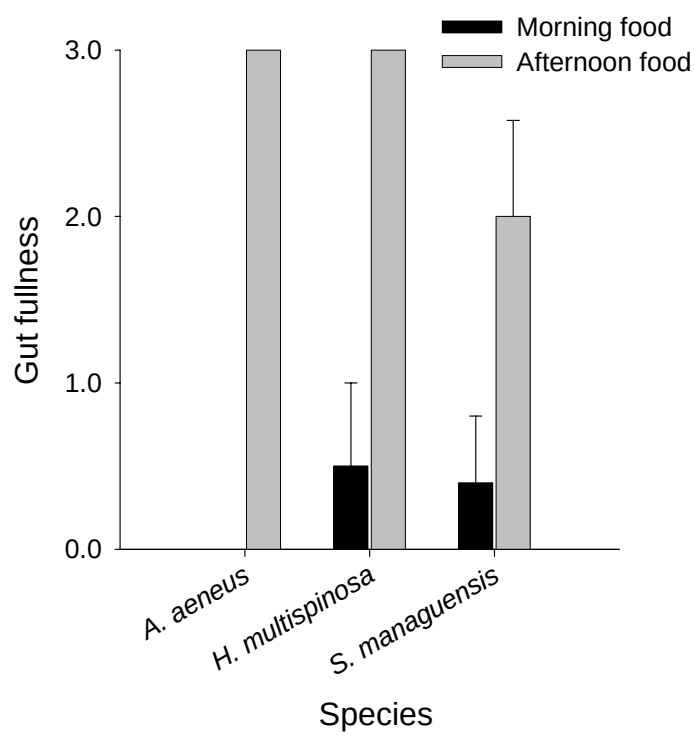

Figure 2. Mean gut content ranking on a scale of 0 to 3 for morning and afternoon samples of three fish species in Palo Verde Marsh. Samples sizes (from left to right) = 2, 2, 4, 1, 5 and 3.

and kingfishers). Predation by crocodilians and fishing bats is highest at night, and bird predation may peak in the early morning when birds are most active (M. Kemp, pers. comm.). Thus, feeding efficacy and predator avoidance may both favor the concentration of feeding activity in the afternoon. Such an alignment of feeding and predator avoidance pressures contrasts with the situation of many organisms, such as dielly migrating zooplankton, which must compromise between activity schedules that maximize feeding rate or minimize predation risk.

Our analysis was limited to shifts of fish abundances within just one marsh habitat type, open water. A future study that utilizes minnow traps, for example, could compare temporal patterns in fish abundances between microhabitats such as open water and floating vegetation. Our interpretation of the data reported here predicts that fish have a diel pattern of migration between open water and protective cover.

The hypothesis that this pattern is caused by both high predation pressures and low feeding efficacy at night and in the early morning would be falsified if predation pressures were actually higher during the day. Any visually feeding piscivorous fish in the marsh and many birds might prey more heavily on fish during the day. Future studies could seek to quantify the strength and diel patterns of predation from specific predators in Laguna Palo Verde.

LITERATURE CITED

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