

Effect of Substrate Type on Fish Distribution in the Rio Claro

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Abstract: Extreme biodiversity of tropical ecosystems with respect to other habitat types has yet to be satisfactorily explained. Our experiments indicate that differences in fish community composition among microhabitats in the Rio Claro of Parque Nacional Corcovado, Costa Rica, may be influenced by differences in abiotic factors. We examined fish communities and physical characteristics of three stream sections. We manipulated substrate type to test for changes in the local distribution of one guild of Gobiidae that was typically associated with cobble substrate. Where cobble substrate was added, abundance of fish taxa belonging to this guild generally increased, and where cobble substrate was replaced with sand, we observed a decrease in abundance. High specialization of these fish to abiotic stream features appears to contribute to high local diversity.

Introduction

The distribution and abundance of tropical freshwater fish species can vary across differing microhabitats (1). This pattern may occur as a function of biotic or abiotic influences or dispersal limitations. Preliminary observations suggested that the highly diverse fish species in one short reach (< 200 m) of the Rio Claro in Parque Nacional Corcovado, Costa Rica were distributed preferentially into one of three distinct habitats - a shallow sandy area, a shallow cobbled area, and a deeper area with a mix of sand, rock, and cobble substrates. In particular, species of the Gobiidae family, which have derived the ability to fix themselves to hard substrate and feed on algae via pectoral fin bones fused into a ventral suction cup (2), were found almost exclusively on cobble and rock substrate.

We hypothesized that differences in fish communities were linked to these differences in abiotic factors among microhabitats, particularly substrate type. Based on this hypothesis, the prediction was made that physical characteristics and fish communities would tend to co-vary in unmanipulated systems and that members of the Gobiidae would shift their positions following substitution of sandy substrate with cobble and vice versa. To determine the patterns of distribution and abundance of these species we created study plots to sample the community.

Methods

We defined the boundaries of 3 adjacent sections of the Rio Claro with apparent physical differences. For each section, we measured approximate area, water velocity at the surface and at mid-column, depth, and temperature.

To quantify substrate type, we drew two 0.25 m² plots, each 2 m to either side of the stream midline, at 10, 25, and 40 m in each section. For each plot, we measured percent cover of 6 substrate types - sand, pebble (1-5 cm diameter), cobble (5-10 cm), rock (10-20 cm), boulder (>20 cm) - and leaf cover. An index of velocity was calculated using the average velocity of 4 suspended objects over 15 m. For surface velocity, we used a floating bottle cap, and for mid-column velocity we used a neutrally buoyant plastic bottle.

We conducted pre-manipulation surveys of fish communities on the afternoons of 3 and 4 February 2004 by snorkeling four 25 m transects in each section. We moved along transects and recorded the number of individuals of each taxon observed within 1 m of the transect.

We manipulated substrate in two 1 m² plots in each section during the morning of 5 February 2004. In sand and pebble-dominated section 1, we created cobble and rock substrate plots. In cobble-dominated section 2, we created sand substrate plots. In sandy-dominated section 3, we created cobble and rock substrate plots. Control plots were located approximately 2 m from the manipulation plots in each section. We sampled taxa in manipulation plots and control plots by counting individuals observed within the plots twice during the afternoon of 5 February 2004 and once on the morning of 6 February.

We used t-tests to look for differences in cobble and stone substrate cover among the 3 pools, and for differences between manipulated plots and controls. We used a 2-way ANOVA to compare abundances of species among stream sections.

Results

The three stream sections had different mean depths, flow velocities, and substrates. Section 1 was intermediate in depth and lowest in velocity; section 2 was lowest in depth and greatest in velocity; section 3 was greatest in depth and intermediate in velocity. Section 2 had significantly higher mean combined cover of cobble and stone substrates (63%) than section 1 (20%) and section 3 (12%) ($F_{2,15} = 11.80, P = 0.0008$).

Species composition of fish communities differed significantly among the three stream sections ($F_{28,111} = 4.57, P < 0.0001$ for species x section interaction). The fish in cobble-dominated section 2 were predominantly cobble-feeding Gobiidae and schools of open water fish

moving through or feeding in the water column. Section 1 contained similar groups of open water fish and a taxon of Gobiidae normally observed only on sandy substrate. Section 3 contained open water fish of the families Cichlidae, Gerreidae, Mugilidae, and Haemulidae, including some species that were never observed in sections 1 and 2. One taxon was found almost exclusively beneath a mat of detritus towards the lower end of section 3.

Cobble-associated species (CAS) generally increased in abundance on cobble addition manipulation plots and decreased on sand addition manipulation plots. CAS appeared in the cobble addition manipulation plots in section 3 ($t = 2.22$, $df = 10$, $P = 0.05$), which otherwise had no CAS. CAS were completely absent from the sand addition manipulation plots in section 2 ($t = 15.07$, $df = 10$, $P < 0.0001$), strongly contrasting high CAS density in adjacent cobble control plots. The cobble addition plots in section 1, however, did not attract a significantly higher number or greater abundance of CAS than adjacent sand and pebble control plots ($t = 0.21$, $df = 10$, $P = 0.84$).

Discussion

Fish communities and physical stream characteristics co-varied among adjacent stream sections, as we predicted. This is consistent with the hypothesis that abiotic factors influence the distribution of stream fish taxa, but does not preclude alternative explanations, such as the influence of temporal species separation on distribution or predation pressure. However, our manipulations of substrate type provide strong evidence for the linkage of fish community composition and abiotic stream features, particularly substrate type.

The correspondence between CAS distribution and the presence of cobble or rock substrate is likely related to the fact that the diet characteristic of CAS consists largely of periphyton (2); periphyton algae grows only on solid substrate (e.g. cobble, not sand) and would presumably grow more densely on rocks or cobbles, which overturn less frequently than smaller substrate like pebbles. In section 1, abundance of CAS did not differ between manipulation and control plots. This may be due either to (I) the close proximity of the cobble (manipulation) habitat to the sand and pebble (control) habitat, or (II)

the availability of periphyton on pebble substrate due to low flow velocity and stable substrate conditions.

Within the Gobiidae alone we observed five morphotypes engaged in what seemed to be identical feeding behavior on the same substrate type. This apparent niche overlap has at least three possible explanations: (I) coexistence of multiple similar species is made possible by very fine partitioning of resources, or (II) similar species are actually functionally identical and are competing unequally, but extinctions are compensated by a high speciation rate (3), or (III) each species has a unique niche and distribution, but they are functionally identical within the study area.

Variation in fish communities among physical environments at such a small scale (< 200 m of stream) is unique to tropical systems. The great variation observed among the different microhabitats of the Rio Claro may evidence a high degree of specialization on particular substrate types may help explain the generally high biodiversity of the tropics. Total fish biomass in this system was also remarkably high compared to northern temperate systems. The combination of high niche partitioning and high biomass suggests a very high resource base of primary production and detritus in the stream system. Future studies should further investigate niche partitioning among similar taxa, such as the cobble feeding Gobiidae, in order to elucidate the exact mechanisms of this partitioning.

REFERENCES

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Note: due to space constraints, appendices were not included in the print edition of this article. For data in excluded appendices, please visit www.dartmouth.edu/~dujs

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