EVALUATING THE EXPLOITATION ECOSYSTEMS HYPOTHESIS IN A MARINE-INFLUENCED RIVER COMMUNITY

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Abstract: According to the Exploitation Ecosystems Hypothesis (EEH), the number of trophic levels in a system predicts the intensity of herbivory on the plant community. We applied this hypothesis to the Río Claro in Corcovado National Park, Costa Rica, where marine predators at high tide may represent an added trophic level. We also hypothesized that herbivorous fish would seek refuge upriver with consequences for trophic structure. We measured percent algal cover and herbivorous fish abundances and recorded substrate type in 1 km transects moving upriver from the mouth. Algal cover declined with increasing distance from the mouth within the tidal zone, and was higher above the tidal zone. Large herbivores were highest in abundance at the upriver edge of the tidal zone, while small herbivores were found exclusively above the tidal zone. The results support the existence of a shift in trophic interactions as predicted by the EEH, but also suggests that trophic structure may be so dynamic that equilibrium may not hold.

Key Words: Gobiidae, Exploitation Ecosystems Hypothesis, tide

INTRODUCTION

The Exploitation Ecosystems Hypothesis (EEH) predicts that herbivore pressure will be directly related to the number of trophic levels in an ecosystem. In ecosystems with an odd number of trophic levels, predators decrease herbivore abundance and green biomass will be high. In ecosystems with an even number of trophic levels, green biomass will be low because of intense herbivory (Oksanen et. al 1981). Many rivers contain two trophic levels: primary producers (algae), and herbivorous fish subject to little or no predation (Oksanen and Oksanen 2000). For example, the Río Claro, near Estación Biológica Sirena, Corcovado National Park, Costa Rica contains herbivorous gobies (Gobiidae) that feed on benthic algae. However, the Río Claro also empties into the Pacific Ocean, permitting large marine predators to enter the river at high tide.

Following the EEH, we hypothesized that the flux of large predators into the tidal zone of the river adds another trophic level and alters herbivore pressure. We predicted that there would be higher algal cover and lower herbivorous fish abundance in the tidal zone compared to the non-tidal zone. We also hypothesized that herbivorous fish move upriver during high tide to avoid marine predators. Thus, we expected that algal cover would be lowest and herbivorous fish abundance would be highest at an intermediate distance from the river mouth immediately beyond the tidal zone.

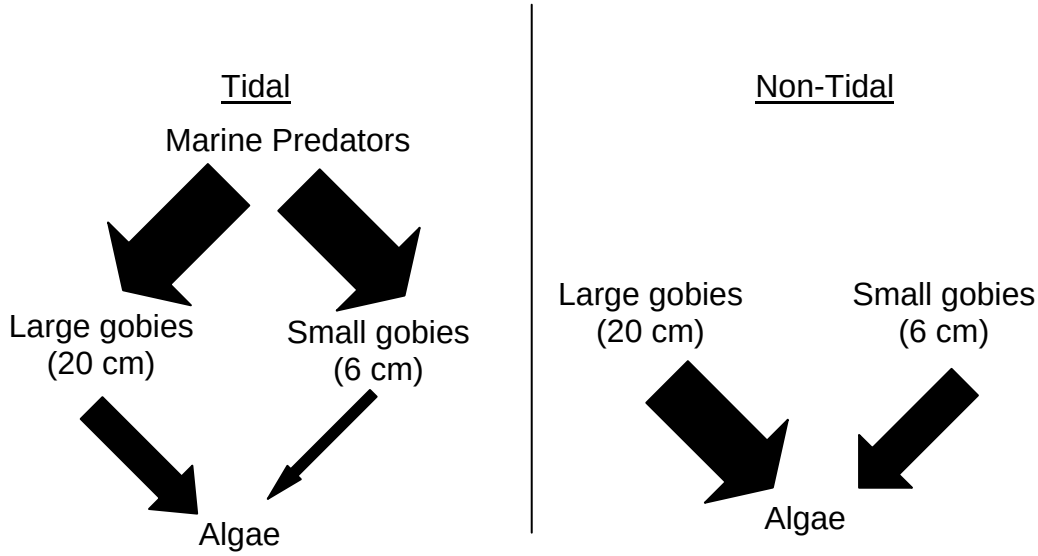

Fig. 1. Trophic structure of the tidal and non-tidal zones in the Río Claro, Corcovado National Park, Costa Rica, as predicted by the Exploitation Ecosystems Hypothesis. Arrow thicknesses represents relative intensities of speculative predation and herbivory.

METHODS

We performed our study on 2 February, 2006 in the Río Claro, Corcovado National Park, Costa Rica. We ran three transects at low tide from the mouth of the river to 1 km upriver. We selected 2 x 2 m plots located every 50 m along each transect, and visually estimated the percent algal cover of the substrate, identified the most prevalent substrate type (cobble, pebble, or sand) and measured water depth. We also recorded the abundance and morphotypes of gobies (Gobiidae), observed within a 5 meter radius during a 2 minutes period.

We employed a general linear model to test how percent algal cover and goby abundances varied with distance from river mouth and substrate. We used chi-square analysis to test for differences in goby abundances between tidal and non-tidal zones. We treated the first 650 m of our transect as the tidal zone based on (1) conductivity samples, and (2) the steepness in topography just after 650 m, which would make intrusion by either salt water or marine predators unlikely. We also looked for relationships between percent algal cover and goby abundances using linear regressions. We used JMP 5.0.1 for all analyses.

RESULTS

We observed changes in the river, both biotic and abiotic, with changes in tide. At high tide, the width of the mouth of the river increased by at least 20 m, and visibility changed from clear to murky. We noted evidence of large marine predators, such as smaller fish jumping and the presence of crocodiles. We conducted our study during a period of extreme variance in tidal levels (low: 21 cm, high: 302 cm).

Within the tidal zone, percent algal cover decreased with increasing distance from the river mouth ($F_{1,8} = 36.43$, $P < 0.001$).

Percent algal cover was again high immediately after the end of the tidal zone (Fig. 2). Substrate explained little or none of the changes in percent algal cover ($F_{2,8}$ = 2.44, P = 0.15).

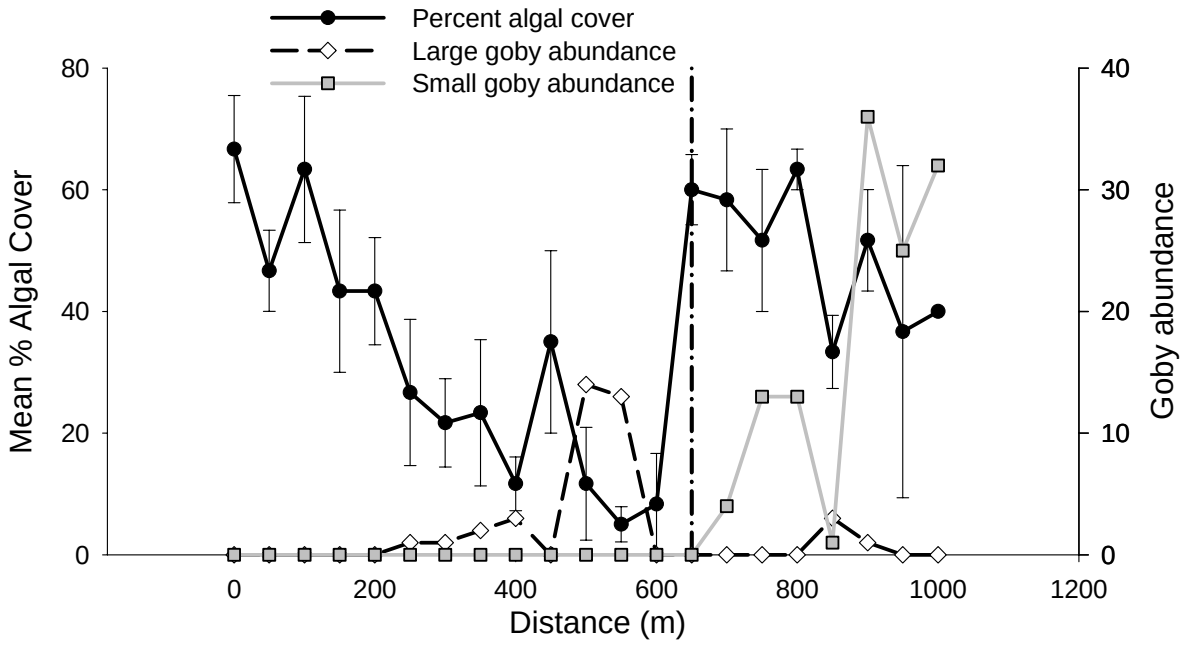

Fig. 2. Mean percent algal cover (± S.E.; black circles, solid black line), large goby abundance (white diamonds, dashed line), and small goby abundance (grey triangle, solid grey line) with increasing distance from the mouth of the Río Claro, Corcovado National Park, Costa Rica. Vertical dashed line at 650 meters represents the division between tidal (left) and above-tidal zones (right).

We observed at least two species of goby: a large species with an estimated length of 20 cm, and a smaller species (or multiple species), with an estimated length of 6 cm, both of which we observed feeding on algae. Large gobies were more abundant in the tidal zone (χ^2 = 201.5, P < 0.001), while small gobies were found exclusively in the non-tidal zone (χ^2 = 12.3, P < 0.001). Percent algal cover decreased with increasing large goby abundance (r^2 = 0.33, df = 19, P < 0.01; Fig. 3), and was still marginally significant after excluding extreme values of 13 and 14 large gobies (r^2 = 0.16, df = 17, P = 0.09; Fig. 3). We found no relationship between percent algal cover and small goby abundance (r^2 = 0.06, df = 19, P = 0.28).

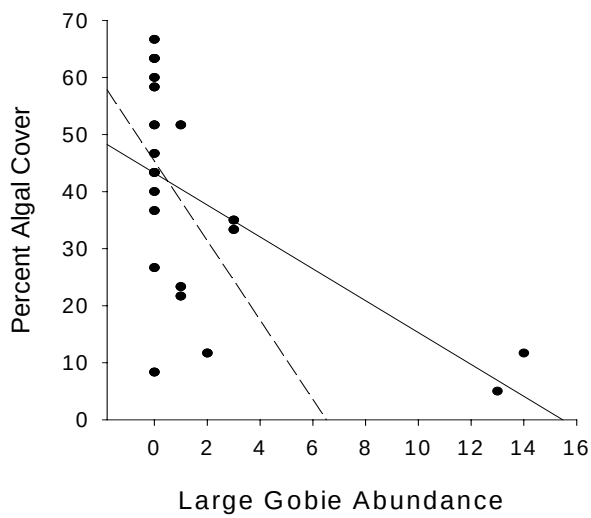

Fig. 3. Percent algal cover by abundance of large gobies in the Río Claro, Corcovado National Park, Costa Rica. Solid regression line (r^2 = 0.33, df = 19, P < 0.01) includes 2 extreme values (x = 13,14), while dashed regression line (r^2 = 0.16, df = 17, P = 0.09) excludes them.

Discussion

Goby and algal distributions and abundances in the Río Claro suggest that the addition of a trophic level has altered herbivory, as predicted by the Exploitation Ecosystems Hypothesis. The absence of gobies and the high percentage of algal cover closest to the river mouth were consistent with the prediction that marine predators drive down herbivorous fish abundances near the mouth. Greater large goby abundances and reduced percent algal cover at the upper end of the tidal zone support the second prediction that herbivorous fish find an upriver refuge from marine predators at an intermediate distance from the mouth. The distribution and abundance of large goby and algae may be a result of both factors: high predation at the mouth and migration to the upper tidal zone at high tide. However, we did not sample at high tide due to greatly reduced visibility and the presence of crocodiles, and we were unable to observe herbivorous fish moving upriver at high tide.

The absence of small gobies in the tidal zone suggests that large predators could have greatly depleted small gobies there. Alternatively, the small gobies may not be adapted to salinity and other conditions in the tidal zone. We acknowledge that our conclusions are speculative, and that many factors in addition to predation vary across the tidal gradient. Examining the salinity tolerance of herbivorous and predatory fish would help to determine the role of salinity in their distribution in the Río Claro.

Literature Cited

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