CORAL PATCHES ON A BACK REEF DO NOT CONFORM TO DIVERSITY-DISTANCE PREDICTIONS OF ISLAND BIOGEOGRAPHY THEORY

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Abstract: The theory of island biogeography has been applied to fish on coral reefs, classifying the larger continuous reef as the "mainland", and patches of isolated coral as "islands", which the theory predicts should have higher diversity as their size increases and their distance from the mainland decreases. However, there is some evidence for the opposite trend with distance, perhaps explained by reduced predation with increasing distance. We tested which of these alternative predictions best matched fish diversity and abundance at isolated coral heads in a back reef on Little Cayman Island, at varying distances from the reef crest. We found that fish diversity and abundance increased significantly with coral patch surface area, consistent with the theory of island biogeography, but decreased with distance, opposite to the prediction of the theory.

Key Words: Island biogeography, Little Cayman, Surface area

INTRODUCTION

The theory of island biogeography predicts the richness of species found on islands of various sizes and distances from a mainland (MacArthur & Wilson 1967, Lomolino 2000). This model assumes that as distance from the mainland increases, the colonization rates of species will be lower, and that extinction rates for species will be higher for smaller islands. Consequently, diversity should decrease with distance, and increase with island size. Molles (1978) found that this theory applied to the diversity of fish on reef patches; larger patches closer to the main reef were more diverse.

However, the opposite trend with distance has also been found. Shulman (1985), reported that fish diversity on reef patches actually increased with isolation. While colonization may follow the trend predicted by island biogeography; decreasing with distance from the main reef (Simberloff & Wilson 1969), there may be greater local extinction near the main reef due to intense predation. Belmaker et al. (2005) showed that high density, mixed-species predatory aggregations (frogfish, jacks, and scorpionfish) were responsible for the local extinction of certain prey fish species, and that these predatory aggregations occurred mainly close to the main reef. Another factor that could increase diversity in patch reefs, relative to the main reef, is the additional food and habitat resource provided by the surrounding sand, where high invertebrate and zooplankton levels have been documented (Ault and Johnson 1998). However, sand habitats and their resources could not explain an increase in diversity with distance from the main reef.

We assumed that colonization would follow the trend predicted by island biogeography theory, and thus predicted juvenile abundance to decrease with distance from the back reef. However, we hypothesized that other factors would result in higher local extinction near the main reef, more than compensating for the colonization-distance trend, and resulting in higher richness and abundance on coral patches further from the continuous back reef. We considered predation the most likely mechanism to drive such a trend in extinction rates, but we did not have the time or resources to test specific mechanisms in this study.

METHODS

From 28 February to 3 March 2008, we sampled 18 coral heads in the lagoon adjoining the Central Caribbean Marine Institute on the north side of Little Cayman Island. We sampled all isolated coral heads shoreward of the strip of continuous back reef, that were within 800 m east or west of CCMI, and a minimum of 2 m from the reef crest. We defined "isolated" as being > 3 m from the nearest coral head.

We counted adults and juveniles of each fish species associated with (within 0.5 m of) each coral head sampled. We measured height and diameter of each coral head to calculate volume (cm^3) and surface area (cm^2), and distance (m) from the main back reef. We visually estimated percent algal cover on each coral head. We will refer to coral heads as "patches".

We used a general linear model to predict fish richness and abundance on patches, using distance from the reef crest and patch surface area as the main effects. We square-root transformed the abundance of each species, number of species, and percent of juveniles for each patch, to meet assumptions of homoscedasticity. Because we had no *a priori* prediction for an interaction (distance x surface area) we removed it from the full model when we found it was non-significant.

RESULTS

Across our samples we tallied 986 fish of 39 species. The average number of species per patch was 14 ± 0.8, and the average number of fish was 54 ± 10.6. Surface area and distance were both positively related to fish abundance and diversity on patches (Table 1).

TABLE 1: Fish species and abundances on coral heads (patches), as a function of distance from back reef, and coral head surface area. Data from 18 coral heads shoreward of the back reef near the Little Cayman Research Center, Little Cayman Island, from February 28th to March 3rd, 2008.

	Fish species diversity			Number of fish		
	F-Value	df	P-Value	F-Value	df	P-Value
Distance	6.66	1	0.02	9.73	1	0.007
Surface area	8.94	1	0.009	7.56	1	0.01
Error		15			15	

Of the 39 fish species we observed, 18 were present only as adults, 1 as juveniles only, and 20 were represented by both juveniles and adults. The overall percentage of fish that were juveniles on a coral patch decreased significantly with distance from the continuous back reef (Figure 1; F = 6.16, df = 1,15, P = 0.02).

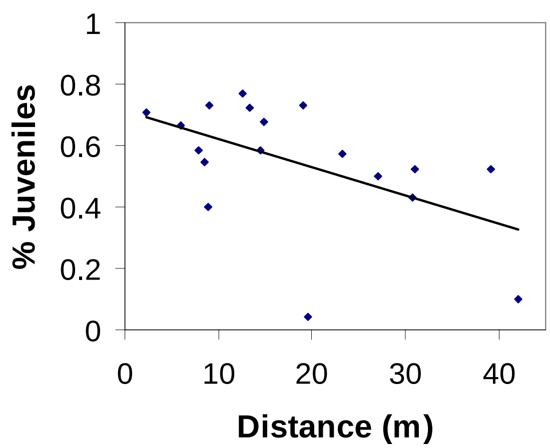

Figure 1. Linear regression of the percent juveniles in fish assemblages on coral heads, plotted against distance (m) from main back reef. Measurements were taken at each of 18 coral heads offshore of the Little Cayman Research Center, Little Cayman Island, from 28 February to 3 March 2008.

DISCUSSION

The theory of island biogeography did not explain all trends that we observed in fish diversity on patch reefs, as a function of distance from the main back reef. As predicted by this theory, abundance did increase with patch surface area; the simple explanation is that with more surface area, there are more refugia and resources available to fish. However, fish diversity and abundance on coral patches actually increased with distance, supporting our hypothesis and conflicting with the theory's predictions.

Trends in abundance and diversity are due to the combination of local colonization and extinction rates. The decrease in percent of juveniles with distance from the main reef (Figure 1) may occur because larvae carried by ocean currents come into contact with the main reef first, with most larvae settling there, decreasing the numbers that colonize more distant patches. We suggest that there is a strong trend in local extinction that counters this colonization trend, with higher rates of extinction closer to the reef. If sufficiently strong, this effect could overcome the presumed trend in colonization, producing the observed positive relationship between distance and fish diversity and fish abundance.

One mechanism that could drive higher extinction rates closer to the reef is predation (Belmaker 2005). Predator density may be higher near the main reef. The extensive reef habitat there may sustain a larger prey population, which can in turn support more predators. Optimal foraging of predators resident on the back reef may contribute to the pattern we observed. Predators may not travel far from the main reef searching for the uncertain and limited resources available on patch reefs, due to low net energy returns.

Our study may be useful in coral reef and fish population management. Knowing the size and distance that artificial reefs should be placed to increase coral reef diversity and abundance can be of practical value in reef restoration.

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