FACTORS DRIVING FISH COMMUNITY COMPOSITION ON PATCH REEF ISLANDS

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Abstract: Large, continuous coral reefs support diverse fish communities, yet the fish community composition of nearby patch reef islands can differ noticeably from the main reef. Island biogeography theory predicts that species richness, abundance, and diversity will increase with increasing patch reef size and distance to a reef-crest source. Alternatively, patch reef species richness, abundance, and diversity may increase with patch size and distance from the reef crest due to decreased predator abundance and diversity away from the reef crest. We tested these somewhat competing hypotheses by investigating patch reef-fish communities in Discovery Bay, Jamaica, and tried to determine which characteristics of patch reefs (distance from reef crest, area, or topographical complexity) are most important in driving fish community composition. We did not find complete support for either hypothesis. The patch reef network in Discovery Bay does not appear to be a simple island system as assumed by both hypotheses, perhaps because overfishing has altered the larger fish community and patch reefs do not function strictly as islands. Patch reef area was the strongest factor driving fish community composition, with species richness and total abundance increasing with area. Species richness and abundance also increased with the interaction between area and complexity. As coral reef communities continue to decline from a combination of natural and anthropogenic pressures, an understanding of the mechanisms driving fish community composition may be crucial for effective management of coral reef fish populations.

Key Words: coral patch reefs, island biogeography, fish community composition

INTRODUCTION

Coral reefs support abundant and diverse fish communities. In the back reef of Discovery Bay, Jamaica, fish communities occur on the coral reef crest mainland and on different-sized patch reef islands, separated from the reef crest by an expanse of turtle grass, where barracuda and other piscivorous fish hunt. Preliminary observations suggested that fish community composition differed both among patch reefs and between the patch reefs and the continuous reef crest. We investigated the relative importance of three putative mechanisms driving the diversity and abundance of fish communities on patch reefs: patch reef area, topographical complexity, and distance from the reef crest.

The equilibrium theory of island biogeography (IBG: MacArthur & Wilson 1967) may explain how fish community composition varies among patch reef islands associated with the coral reef mainland. The theory predicts that island species richness will decrease with increasing distance from a mainland source because more remote islands receive fewer immigrants. An addition to the theory known as the target effect suggests that species richness will increase with island size because large islands are larger targets for immigrants from the mainland (Whitehead & Jones 1969).

We hypothesized that fish species richness on patch reefs will increase with increasing patch reef area and proximity to the continuous coral reef crest. We also hypothesized that fish abundance and diversity would follow similar trends and increase with island size and proximity to the reef crest.

Alternatively, fish species richness, abundance and diversity may increase on patch reefs located farther from the reef crest. In contrast to IBG theory, Belmaker et al. (2005) found that species richness on isolated patch reefs increased with distance from a natural, continuous fore reef, because predators may be more abundant and diverse on continuous reefs where fish populations are larger and can support more predators. Isolated patch reefs farther from the continuous reef crest may provide a refuge from predation and thus harbor higher species richness, abundance, and diversity than proximate patch reefs of equal size. Because predator abundance and diversity may also increase with increasing patch reef area, large patch reefs may have decreased species richness, abundance and diversity.

Small reef fish may have more success avoiding predators in patch reefs with greater structural complexity, if greater complexity offers fish more refuge sites. Complex patch reefs may also support a larger food base due to a higher recruitment of algae and marine invertebrates (Almany 2004; Bizzarro 1992). Therefore, we hypothesized that species richness, abundance and diversity will increase with increasing topographical complexity of patch reefs.

METHODS

On 3-5 March 2006, we identified patch reefs by following four 20 x 50 m transects perpendicular to and 10 m from the reef crest, and selecting patch reefs along each transect that were isolated from one another by at least 2 m. To avoid confounding the reef crest source of fish with any potential shore source, we only observed patches in the section of reef separated from the shore by a large, deep section of open water.

We measured the length, width, complexity, and distance from the reef crest of each patch reef. The shape of the patch reefs generally resembled an ellipse, so we approximated patch reef area with the formula π x length x width. We determined patch reef complexity by tracing the topographical surface of each patch reef with a metal chain along the same lines at which we measured length and width. We then generated a complexity index (rugosity) for each patch reef using the equation rugosity = complexity / [(2 x height) + (length or width)] and averaging the rugosity of length and width measurements.

We monitored each patch reef for 5 minutes, recording all observed fish and determined the total fish abundance and species richness of each patch reef. We used these data to calculate the Gini diversity index,

$$I = 1 - \sum_{i=1}^{n} p_i^2$$

[Eq. 1]

for each patch reef, where *I* is the probability that two randomly selected individuals from a community are of different species, and *p* is the proportion of individuals on a patch reef belonging to one species.

We analyzed the effect that patch reef area, complexity, and distance from the reef crest had on patch reef species richness, abundance, and diversity by using a simple linear model in JMP 5.0.1. We checked for covariation of predictors and transformed data where necessary to meet the condition of normality.

RESULTS

We observed 40 patch reefs with areas varying from 0.10 m^2 to 16.6 m^2 at distances of 11.5 m to 66 m from the reef crest. We found patch reefs supporting 0 to 86 fish and up to 12 species of the 26 total fish species we observed.

Patch reef area was the strongest factor explaining fish community composition: increasing patch reef area predicted increasing species richness ($F_{1,39}$ = 7.63, P = 0.01) and greater abundance ($F_{1,39}$ = 12.40, P < 0.01). Species richness and abundance also increased with the interaction between increasing patch reef complexity and area (richness: $F_{1,39}$ = 4.29, P= 0.05, abundance: $F_{1,39}$ = 6.65, P = 0.01), but not with complexity alone (P > 0.45). Distance from reef alone was not a predictor of richness, abundance, or diversity (all P > 0.15).

Although abundance increased with patch reef area, the relative abundance of fish (# fish /m^2) decreased with increasing patch reef area ($F_{1,37}$ = 5.20, P = 0.03; Fig. 1). Similarly, relative species richness decreased with increasing patch reef area ($F_{1,37}$ = 17.3, P < 0.001; Fig. 2).

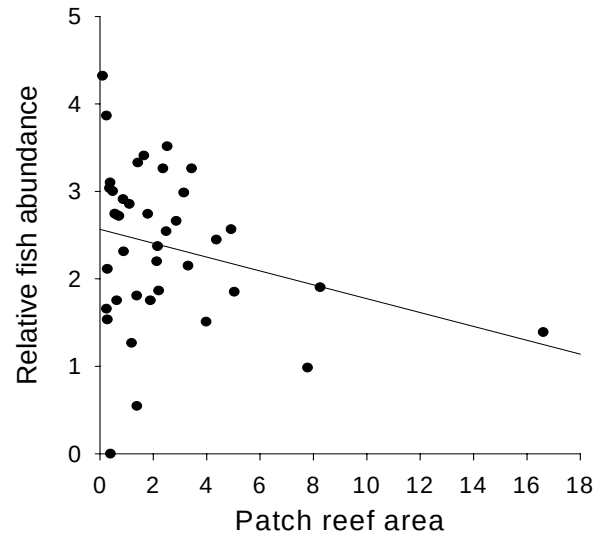

Figure 1. Relative fish abundance, *Ln [(fish abundance / patch reef area) + 1]*, as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish abundance decreases with increasing patch reef area (r^2 = 0.12, df = 37, P = 0.03).

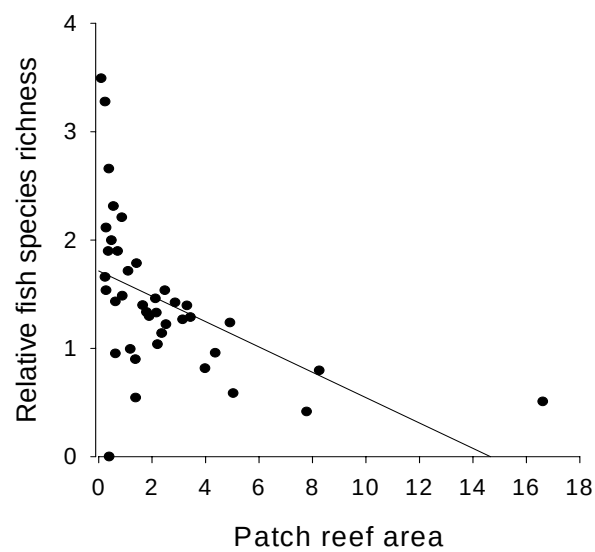

Figure 2. Relative fish species richness, *Ln [(fish species richness / patch reef area) + 1]*, as a function of reef patch area in the back reef off of Discovery Bay Marine Laboratory, Jamaica. Relative fish species richness decreases with increasing patch reef area (r^2 = 0.32, df = 37, P < 0.001).

Table 1. Effect of various patch reef characteristics (patch reef area, topographical complexity, and distance from reef crest) on (A) fish species richness, (B) total fish abundance [*Ln (fish abundance + 1)]*, and (C) Gini diversity index [*Ln (Gini diversity index + 1)]*, for reef patches extending in from the back reef at Discovery Bay Marine Laboratory, Jamaica. Statistics were generated using a general linear model of patch reef characteristics and interactions between the characteristics. Boldface type indicates significant effect.

A. Effect on fish species richness

Effect	Sum of squares	$F_{1,39}$	P
Area	**42.7**	**7.63**	**0.01**
Complexity	2.91	0.52	0.48
Distance	12.2	2.18	0.15
Area*Complexity	**24.0**	**4.29**	**0.05**
Area*Distance	1.34	0.24	0.63
Distance*Complexity	2.89	0.52	0.48
Distance*Area*Complexity	0.75	0.13	0.72

B. Effect on normalized total fish abundance

Effect	Sum of squares	$F_{1,39}$	P
Area	**8.69**	**12.4**	**0.001**
Complexity	0.27	0.38	0.54
Distance	0.92	1.32	0.26
Area*Complexity	**4.65**	**6.65**	**0.01**
Area*Distance	2.36	3.38	0.08
Distance*Complexity	0.08	0.12	0.74
Distance*Area*Complexity	0.46	0.66	0.42

C. Effect on normalized Gini diversity index

Effect	Sum of squares	$F_{1,38}$	P
Area	0.06	1.72	0.20
Complexity	0.03	0.80	0.38
Distance	0.003	0.10	0.76
Area*Complexity	0.02	0.49	0.49
Area*Distance	0.04	1.18	0.29
Distance*Complexity	0.001	0.04	0.84
Distance*Area*Complexity	0.03	0.90	0.35

DISCUSSION

We did not find complete support for either of the competing hypotheses potentially explaining how patch reef area and distance from the reef crest should influence fish community composition. Patch reef species richness and abundance increased with patch reef area, consistent with IBG theory. However, large patches hosted fewer species per unit area than small patches. Therefore, we could not distinguish between the hypothesis that large islands support more abundant, speciose fish communities and the possibility that abundance and species richness simply increased with increasing sample area, a result that would have been expected regardless of whether patch reefs functioned as islands.

The lack of direction in the effect of distance from reef crest on community composition supports neither IBG theory nor the predator risk hypothesis of Belmaker et al. (2005). We suggest that the severe overfishing in Discovery Bay has

removed many top predators from the ecosystem, altering the effects of patch characteristics on fish community composition. For instance, in contrast to Belmaker et al. (2005), predator density at Discovery Bay may be equally low throughout the back reef. Therefore, more distant islands may not provide increased isolation from predators, and there is no trend of corresponding increased fish species richness. Predator scarcity also allows for an increased flow of fish both between patch reefs and between the reef crest and the patch reefs; thus these patch reefs may not act as isolated islands. If there is high species flow between these patch reefs, IBG theory alone cannot explain fish community composition.

The significant interaction effect of area and complexity suggests that larger, more complex patch reefs can support higher fish abundance and species richness than smaller, less complex reefs. Large, complex reefs can potentially provide a greater number of habitats and therefore can support a higher number of individuals and species.

Quantifying the relative importance of factors driving communities of fish on patch reefs will provide an understanding of how patch reefs can support and sustain fish populations. As coral reef communities continue to decline from a combination of natural and anthropogenic pressures, an understanding of the mechanisms driving fish community composition may be crucial for effective management of coral reef fish populations.

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