# FISH AND CORAL COMMUNITY STRUCTURE ARE RELATED ON SHALLOW WATER PATCH REEFS NEAR SAN SALVADOR, BAHAMAS

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## ABSTRACT

We measured abundance and diversity of fishes and corals at three patch reef complexes near San Salvador, Bahamas, and examined relationships among species and ecological measures of fish and coral community structure. Generalized Discriminant Analyses indicated which ecological variables distinguished reefs and which fish and coral species accounted for observed differences among reefs. Canonical Correlation Analysis revealed relationships between fish and coral species at each reef. Reefs with the greatest coral cover had the highest abundance and species richness of fishes. These results add to studies describing relationships between reef fishes and corals, and establish a benchmark for fish and coral community structures and relationships near San Salvador in the Bahamas during a time of region-wide declines of Caribbean corals.

The physical complexity of coral reefs provides a myriad of microhabitats supporting numerous fish species, many of which are site-attached or strongly tied to reef habitats. Coral abundance, diversity, or cover may influence the resident fish community by providing increased reef surface area or structural complexity. Fish abundance has been positively correlated with scleractinian corals responsible for the construction of reefs (Bell and Galzin, 1984; Lirman, 1999). In Caribbean waters, gorgonians are prominent members of the coral community and may provide additional microhabitat or cover for fish species or, conversely, discourage the presence of certain species either by displacing important scleractinians or through chemical deterrence (Goldberg, 1973). Furthermore, decreased live coral cover has been associated with an increased abundance of herbivorous fishes, presumably due to increased algal cover (Bell and Galzin, 1984; Galzin, 1987; Carpenter, 1990; Gladfelter et al., 1991a,b; Lirman, 1999).

Fish-habitat associations on coral reefs are well documented; previous work has shown linkages between fish abundance and microhabitat availability (Caley and St. John, 1996), habitat complexity (Jones, 1988), habitat abundance (Tolimieri, 1998) and richness (Ault and Johnson, 1991), substratum diversity (Gladfelter and Gladfelter, 1978; Roberts and Ormand, 1987), live coral (Garpe and Öhman, 2003), and algal community structure (Chittaro, 2004). However, several studies have not supported such relationships (Luckhurst and Luckhurst, 1978; Molles, 1978; McManus et al., 1981; Lewis and Wainwright, 1985; Roberts and Ormond, 1987; Bohnsack et al., 1992; Syms and Jones, 2001), possibly due to sampling-scale issues, diverse sampling methodologies, or lack of powerful statistical analysis tools.

We tested for abundance and diversity relationships between fish and coral communities on contrasting shallow-water patch reefs using non-destructive, underwater visual surveys near San Salvador, Bahamas (Walter, 2002). We compared three regions known to differ in terms of percent coral cover and diversity (McGrath and Smith, 2003). Our objective was to determine whether reef fish community struc-

ture could be related to selected aspects of coral community structure. Using data collected from all reefs, we also examined relationships between abundant fish and coral species.

## Methods

Study Reefs.— Patch reef complexes from three regions near San Salvador were selected for surveys of fishes and corals. Each complex consisted of three or more patch reefs < 50 m apart and separated by sand flats. Lindsay Reef (three patches) is a leeward reef on the west side of the island; Rocky Point (four patches) is a windward reef on the northwest corner of the island; and Rice Bay (three patches) is a windward reef on the northeast corner of the island (Fig. 1). Samples were collected on multiple patches in each complex and the overall area of each complex was roughly the same, as estimated visually.

Faunal Surveys and Data Analysis.— In December 2000 and January 2001, we conducted surveys to determine dominant coral species and topographic complexity (rugosity). Rugosity was measured at 10 sites on each reef complex by dividing the length of a line draped over 5 m of bottom by 5 m; higher ratios indicated greater topographic complexity (McGrath and Smith, 2003). In May and June 2001, we randomly placed 16 10 × 5 m plots on each of the three reef complexes. Fish were sampled by underwater visual surveys within these plots following Lirman (1999). We observed large individuals and aggregations from two points (2.5 min each) halfway along the periphery of the long axis for each plot. For site-attached or demersal fishes, we conducted swimming surveys along two, 10 × 2.5 m transects within each plot. Counts from the four point and swimming surveys were combined and averaged to provide one estimate of fish species abundance per plot. Live coral cover also was visually estimated within each 10 × 5 m plot using ten, 1 m$^2$ haphazardly placed quadrats. Within each quadrat, we visually estimated the percent cover for each scleractinian species, canopy cover for gorgonians in aggregate and total algal cover, using the scale of Ormond et al. (1996): < 0.1%, 0.1%–1%, 1%–10%, 11%–25%, 26%–50%, 51%–75%, 76%–90%, 91%–99%, 100%. Data from the 10 quadrats were used to estimate mean cover values for each species or group in each 10 × 5 m plot (Walter, 2002).

Diversity (Shannon's $H'$) and equitability ($E$) were computed for the coral and fish communities following Magurran (1988). Generalized Discriminant Analysis (GDA) using Canonical
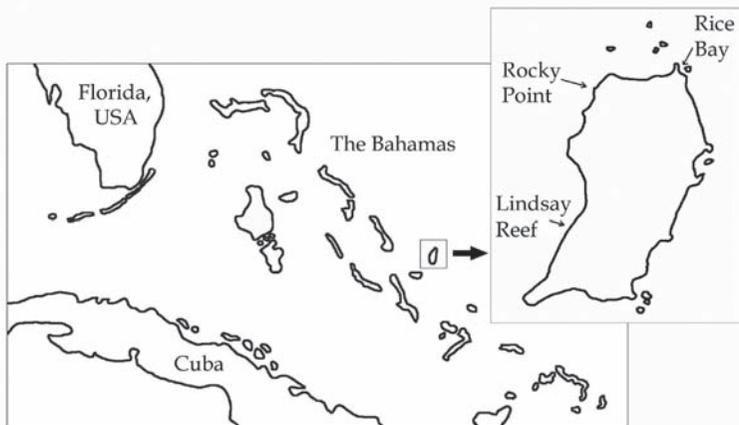


Figure 1. Locations of the three study reef complexes, Rice Bay, Rocky Point and Lindsay Reef, near San Salvador, Bahamas.

Table 1. Fish and coral data from three patch reef complexes (n = 16 sample plots per complex) near San Salvador, Bahamas. **P < 0.01 and *P < 0.05 after post-hoc ANOVA and Bonferroni corrections for multiple comparisons within variables.

| | Rice Bay | | Rocky Point | | Lindsay reef | |
|---|---|---|---|---|---|---|
| | Mean | SE | Mean | SE | Mean | SE |
| Fish abundance (50 m$^{-2}$) | 23.0** | 3.2 | 45.6 | 1.7 | 47.1 | 4.4 |
| Fish species richness | 8.7* | 1.1 | 10.3 | 0.5 | 13.3 | 0.8 |
| Fish Shannon $H'$ | 1.72 | 0.10 | 1.71 | 0.10 | 2.10 | 0.07 |
| Fish equality $E$ | 0.57 | 0.01 | 0.74** | 0.01 | 0.55 | 0.02 |
| Scleractinia cover (%) | 1.2** | 0.27 | 3.7 | 0.54 | 4.7 | 0.40 |
| Gorgonacea cover (%) | 1.5** | 0.47 | 4.7 | 0.79 | 3.2 | 0.52 |
| Coral species richness | 11.9 | 1.17 | 14.3 | 0.67 | 14.6 | 0.51 |
| Coral Shannon $H'$ | 1.61 | 0.17 | 1.92 | 0.06 | 1.93 | 0.07 |
| Coral equitability $E$ | 0.69 | 0.06 | 0.73 | 0.02 | 0.98** | 0.09 |
| Algal cover | 60.3** | 0.78 | 46.7 | 0.58 | 48.9 | 0.27 |
| Rugosity | 0.16* | 0.03 | 0.28* | 0.03 | 0.41* | 0.05 |

Analysis of Principal Coordinates (CAP: Anderson and Willis, 2003; Anderson and Robinson, 2003) was used to test for significant differences in the fish and coral communities among the reefs. All CAP analyses were performed using the Bray-Curtis distance matrix and canonical test statistics were obtained via permutation tests (9999 permutations). ANOVA with Tukey's post-hoc multiple comparisons tests (with Bonferroni corrections) was performed to establish which reefs differed in terms of diversity and abundance of fishes and corals. Where applicable before ANOVA, fish and coral data were ln $(x + 1)$ and arc-sine square-root transformed, respectively. Canonical Correlation Analysis using CAP (Anderson and Willis, 2003; Anderson and Robinson, 2003) was used to test for relationships between fish species abundance and coral species cover across the reef complexes.

## Results

Thirty-six coral and 57 fish species were observed at the three reef complexes (Walter, 2002). Algal cover was significantly higher at Rice Bay than at the other sites (P < 0.01; Table 1). Rugosity was significantly higher at Lindsay Reef than at the other reefs and at Rocky Point than at Rice Bay (P < 0.05; Table 1). Fish abundance and species richness were significantly lower at Rice Bay than at Lindsay Reef and Rocky Point, equitability was significantly higher at Rocky Point that at the other reefs, and there was a trend (0.05 < P < 0.1) of higher Shannon's diversity at Lindsay Reef than at the other reefs.

GDA revealed significant differences ($\delta_1^2 = 0.776$, P = 0.0001) in the fish assemblage structure at each reef (Fig. 2A); 41.4% of the variance in fish abundance was explained by the first two principal coordinate axes. Correlations of abundant fish species with CV1 and CV2 (the vectors in Fig. 2B) account for the differences in fish assemblage structure among reefs (the locations of reefs in different quadrants in Fig. 2A). The most common species were *Stegastes leucostictus* (Muller and Troschel, in Schomburgk, 1848), *Halichoeres bivittatus* (Bloch, 1791), *Malacanthus plumieri* (Bloch, 1786), and *Chaetodon ocellatus* (Bloch, 1787) at Rice Bay; *Acanthurus coeruleus* (Bloch and Schneider, 1801), *Acanthurus chirurgus* (Bloch, 1787), *Microspathodon chrysurus* (Cuvier, in Cuvier and Valenciennes, 1830), *Ophioblennius atlanticus* (Valenciennes, in Cuvier and Valenciennes, 1836), and *Stegastes variabilis* (Castelnau, 1855) at Rocky Point; and *Scarus iseri* (Bloch, 1789), *Pseudupeneus maculatus* (Bloch,
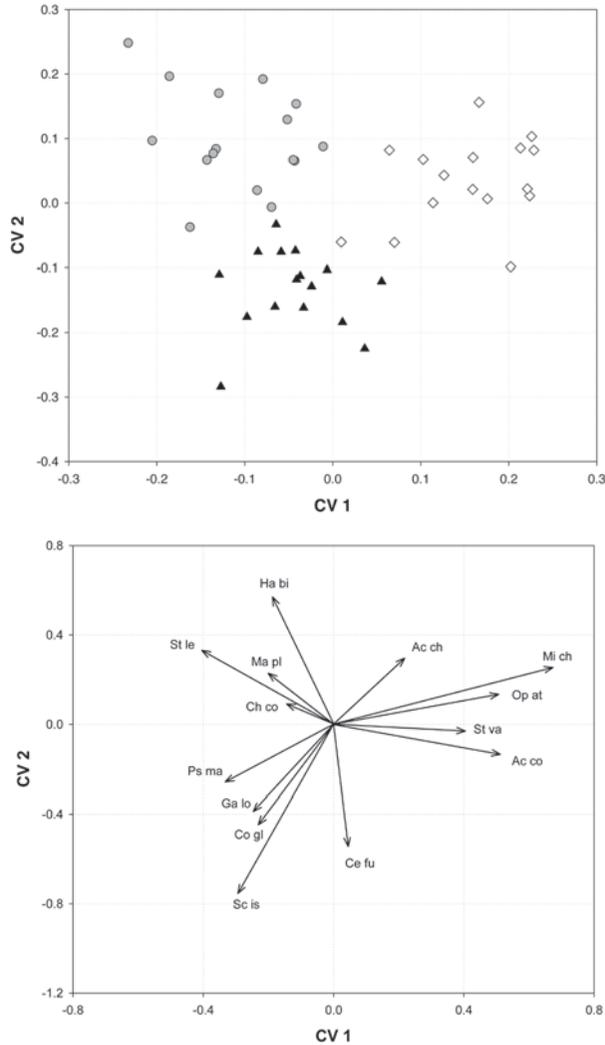
Figure 2. (A). Generalized Discriminant Analysis plot showing differences in the distribution of fish abundances at three patch reef complexes near San Salvador, Bahamas. (B) The fish species most common at each reef complex with the canonical variates. Rice Bay [O]: *Stegastes leucostictus* (St le), *Halichoeres bivittatus* (Ha bi), *Malacanthus plumieri* (Ma pl), *Chaetodon ocellatus* (Ch oc); Rocky Point [◇]: *Acanthurus coeruleus* (Ac co), *Acanthurus chirurgus* (Ac ch), *Microspathodon chrysurus* (Mi ch), *Ophioblennius atlanticus* (Op at), *Stegastes variabilis* (St va); Lindsay Reef [△]: *Scarus iseri* (Sc is), *Pseudupeneus maculatus* (Ps ma), *Gramma loreto* (Gr lo), *Coryphopterus glaucofraenum* (Co gl), *Cephalopholis fulva* (Ce fu).

1793), *Gramma loreto* (Poey, 1868), *Coryphopterus glaucofraenum* (Gill, 1863), and *Cephalopholis fulva* (Linnaeus, 1758) at Lindsay Reef.

Scleractinian cover was significantly lower at Rice Bay than at Lindsay Reef and Rocky Point, gorgonian cover was significantly lower at Rice Bay than at Rocky Point, and coral equitability was significantly higher at Lindsay Reef than at the other reefs (P < 0.05; Table 1). There was a trend (0.05 < P < 0.1) of lower coral species richness and Shannon's diversity at Rice Bay than at Lindsay Reef and Rocky Point.
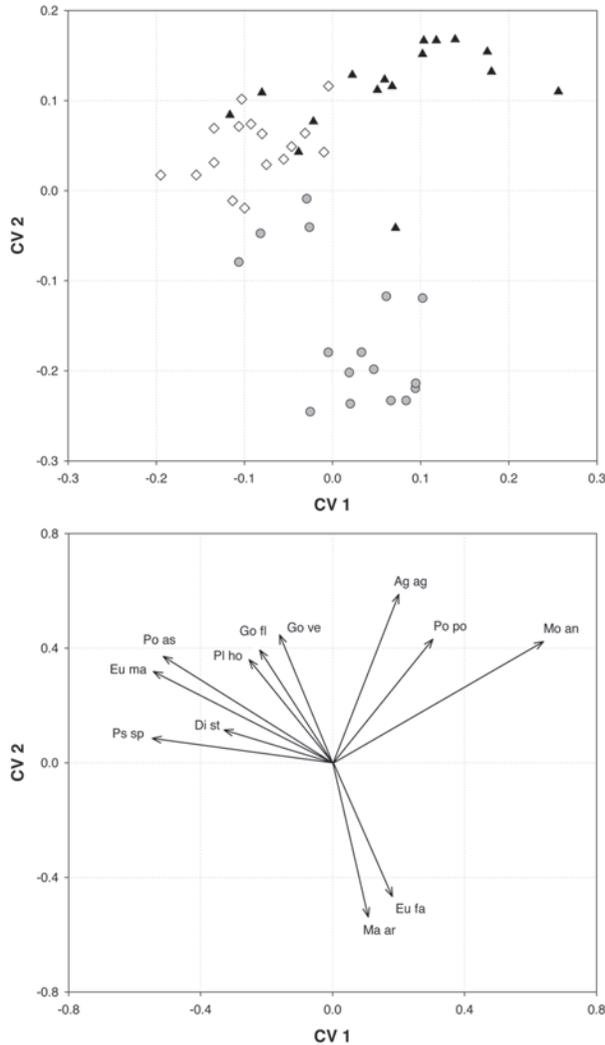
Figure 3. (A) Generalized Discriminant Analysis plot showing differences in the distribution of coral cover at three patch reef complexes near San Salvador, Bahamas. (B) Correlations of the coral species most common at each reef complex with the canonical variates. Rice Bay [O]: *Eusmilia fastigiata* (Eu fa), *Manicina areolata* (Ma ar); Rocky Point [◇]: *Pseudoplexaura* sp. (Ps sp), *Gorgonia ventalina* (Go ve), *Gorgonia flabellare* (Go fl), *Plexaura homomalla* (Pl ho), *Porites astreoides* (Po as), *Eunicea mammosa* (Eu ma) and *Diploria strigosa* (Di st); Lindsay Reef [△]: *Montastraea annularis* (Mo an), *Agaricia agaricites* (Ag ag) and *Porites porites* (Po po).

GDA revealed significant differences ($\delta_1^2 = 0.294$, P = 0.001) in coral assemblage structure at each reef (Fig. 3A); 40.8% of the variance was explained by the first two principal coordinate axes. Correlations of abundant coral species with CV1 and CV2 (the vectors in Fig. 3B) account for the differences in coral assemblage structure among reefs (the locations of reefs in different quadrants in Fig. 3A). The most common coral species were *Eusmilia fastigiata* (Pallas, 1766) and *Manicina areolata* (Linneaus, 1758) at Rice Bay; *Pseudoplexaura* sp., *Gorgonia ventalina* (Linneaus, 1758), *G. flabellare* (Linneaus, 1758), *Plexaura homomalla* (Esper, 1792), *Porites astreoides* (Lamarck, 1816), *Eunicea mammosa* (Lamouroux, 1816) and *Diploria strigosa* (Dana,
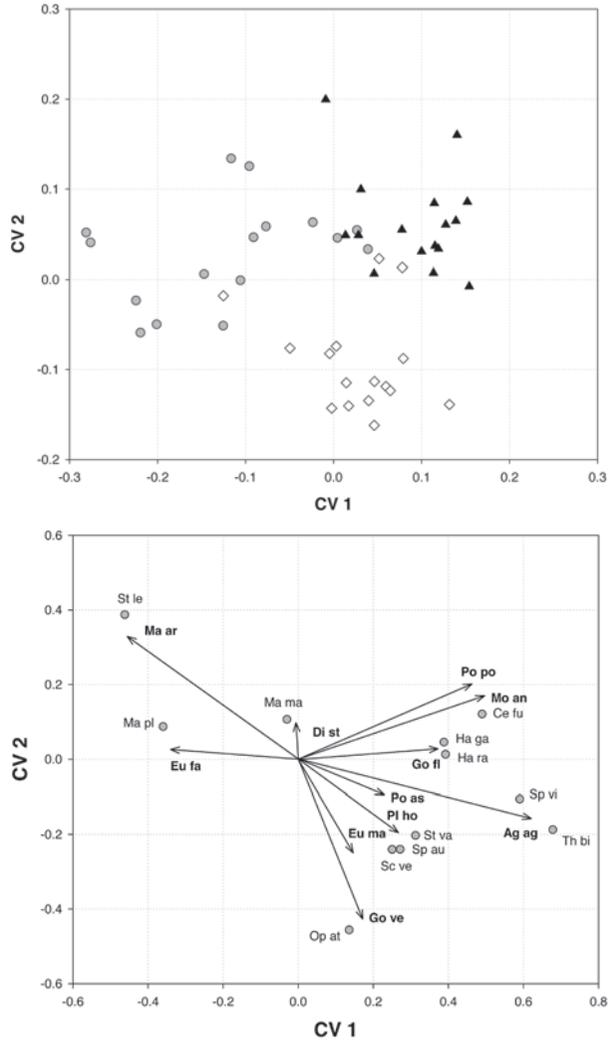
Figure 4. Canonical Correlation Analysis plot showing significant correlations between fish abundance and coral cover at each reef complex. (A) Position of the reef complexes along the canonical variates (O: Rice Bay; ◇: Rocky Point △: Lindsay Reef). (B) Loadings of fish and coral species along the canonical variates. Vectors represent coral species; circles represent fish species. Fish: *Cephalopholis fulva* (Ce fu), *Halichoeres garnoti* (Ha ga), *Halichoeres radiatus* (Ha ra), *Malacanthus plumieri* (Ma pl), *Malacoctenus macropus* (Ma ma), *Scarus vetula* (Sc ve), *Sparisoma aurofrenatum* (Sp au), *Sparisoma rubripinne* (Sp ru), *Sparisoma viride* (Sp vi), *Stegastes variabilis* (St va), *Stegastes leucostictus* (St le), *Stegastes planifrons* (St pl), *Thalassoma bifasciatum* (Th bi). Corals: *Agaricia agaricites* (Ag ag), *Diploria strigosa* (Di st), *Eusmilia fastigiata* (Eu fa), *Eunicea mammosa* (Eu ma), *Gorgonia flabellare* (Go fl), *Gorgonia ventalina* (Go ve), *Manicina areolata* (Ma ar), *Montastraea annularis* (Mo an), *Plexaura homomalla* (Pl ho), *Porites astreoides* (Po as), *Porites porites* (Po po).

1846) at Rocky Point; and *Montastraea annularis* (Ellis and Solander, 1786), *Agaricia agaricites* (Linnaeus, 1758) and *Porites porites* (Pallas, 1766) at Lindsay Reef.

Canonical Correlation Analysis revealed significant relationships ($\delta_1^2 = 0.624$, P = 0.0007) between fish species abundance (extracted by GDA; Fig. 2B) and coral species cover (extracted by GDA; Fig. 3B) at each reef (Fig. 4A). Three fish species were associated with coral species at Rice Bay: *S. leucostictus* with *M. areolata*, *M. plumi-*

*eri* with *E. fastigiata,* and *Malacoctenus macropus* (Poey, 1868) with *D. strigosa*. Five fish species were associated with coral species at Rocky Point: *O. atlanticus* with *G. ventalina* and *Scarus vetula* (Bloch and Schneider, 1801), *Sparisoma aurofrenatum* (Valenciennes, in Cuvier and Valenciennes, 1840) and *S. variabilis* with *P. homomalla* (and somewhat with *E. mammosa* and *P. astreoides*). Three fish species were associated with coral species at Lindsay Reef: *C. fulva* with *M. annularis* (and somewhat with *P. porites*) and *Halichoeres garnoti* (Valenciennes, in Cuvier and Valenciennes, 1839) and *H. radiatus* (Linnaeus, 1758) with *G. flabellare*. *Thalassoma bifasciatum* (Bloch, 1791) and *Sparisoma viride* (Bonnaterre, 1788) were associated with *A. agaricites* at Rocky Point and Lindsay Reef (Fig. 4B).

## Discussion

We found distinct differences in the structure of fish (abundance and diversity measures) and coral communities (cover and diversity measures) at three patch reef complexes near San Salvador, Bahamas. Also, reefs with higher coral cover had higher fish abundance. The reefs we studied were chosen *a priori* for known differences in physical conditions and coral cover (McGrath and Smith, 2003). Lindsay Reef, the leeward reef, had less wave exposure and turbidity than Rocky Point or Rice Bay and the most equitable distribution of coral species. However, greater coral equitability at Lindsay Reef did not translate into greater equitability of fish species abundances. Rice Bay, with the least favorable conditions for corals, had the least equitable distribution of coral species and the lowest coral cover. A windward reef, Rice Bay has been subjected to higher turbidity during the past 20 yrs (McGrath and Smith, 2003). The less abundant and diverse fish community at Rice Bay may be responding to the more difficult conditions for corals compared to Lindsay Reef. Interestingly, the greater number of significant relationships between fish abundance and coral variables at disturbed than at undisturbed reefs has been noted in earlier studies (Chabanet et al., 1997; Syms and Jones, 2000). Rocky Point appears to be a physico-geographic intermediate between Lindsay Reef and Rice Bay with intermediate fish species richness, scleractinian cover and coral equitability values.

Significant associations between the abundance of individual fish and coral species were noted at each reef. These relationships may reflect selection or avoidance by fishes of the general habitats at the sites we studied or of specific characteristics of the coral species in those habitats. For example, the association of *M. plumieri* with *E. fastigiata* may occur because the fish burrows exclusively in sand and the coral is tolerant of turbidity and found in sandy areas. The association of *T. bifasciatum* and *S. viride* with *A. agaricites* likely reflects an edge effect, as both species are commonly found at the edge of reefs, but also may indicate association with areas with higher structural complexity. Chittaro (2004) found positive associations between *T. bifasciatum* and dead *Acropora palmata*, dead *M. annularis*, the alga *Padina jamaicensis* ((Collins), in Papenfuss, no date) and structural complexity at St. Thomas, USVI. Chittaro (2004) also reported positive relationships between *S. viride* and the abundance of live and dead *P. porites* at larger spatial scales (200 and 1000 m$^2$) than we sampled.

We report a positive relationship between *S. leucostictus* and cover of *M. areolata* at Rice Bay, in contrast to observations of positive relationships with areas of dead *M. annularis* in St. Thomas, USVI (Booth and Beretta 1994). Lirman (1999) reported

negative relationships between S. *leucostictus* and coral cover in Florida, St. Thomas, and St. Croix, USVI, results which may be congruent with our observations since *M. areolata* typically occurred in areas otherwise depauperate of coral cover, probably due to its tolerance of sedimentation.

Some fish-coral associations may also be due to the dominance of particular coral species at a reef. For example, the association of *S. aurofrenatum*, *S. vetula* and *S. variabilis* with the gorgonian *P. homomalla* may be due to high overall abundance and even distribution of *P. homomalla* across samples at Rocky Point. Other associations appear unclear, for example, the association of *O. atlanticus* with *G. ventalina* at Rocky Point. However, Wilson (2001) found a high proportion of blennies on reef tops and non-living coral, and at least partially related their abundance to availability of detritus. Associations also may reflect trophic relationships: the association of the piscivore *C. fulva* with *M. annularis* and *P. porites* at Lindsay Reef may indicate that those corals support higher numbers of prey (Bell and Galzin, 1984).

Fish species richness was intermediate, and equitability of their abundances was highest, at Rocky Point where gorgonian cover was highest. Previous work has noted higher catches of exploitable fish species in traps set adjacent to gorgonian habitats (Wolff et al. 1999). The association of *S. vetula* and *S. aurofrenatum* with the gorgonians *P. homomalla* and *E. fastigiata* at Rocky Point may reflect the fishes' preferences for gorgonian habitat during daylight hours (Ogden and Buckman, 1973; Wolff et al., 1999).

Interactions among benthic and coral community attributes (Gladfelter and Gladfelter, 1978; Roberts and Ormand, 1987; Caley and St. John, 1996; Chittaro, 2004), density-dependent factors within the fish community itself (Jones, 1988), or density-independent and physico-geographic parameters (Jones 1991; Montgomery et al., 2001;) all potentially affect fish assemblages on a coral reef. Our results are consistent with the idea that aspects of coral community structure influence the structure of fish communities on small patch reefs. Although variation in the distribution and abundance of both fishes and corals was marked across our study locations, it appears that reefs with higher coral cover support higher abundances and species richness of fishes.

Finally, coral reefs are in decline worldwide (Hughes et al., 2003) and especially in the Caribbean (Gardner et al., 2003). Reefs near San Salvador are no exception. They suffered the Caribbean-wide, precipitous decline of *Diadema antillarum* in the 1980s (Carpenter, 1990), and average scleractinian cover near the island has declined from ~20% in the 1980s to ~4%–5% today (Walter, 2002; McGrath and Smith, 2003). In addition, San Salvador is developing rapidly economically, with an approximately three-fold increase in population and associated fishing effort since 1992. Our study establishes a benchmark for fish and coral community structures and relationships near San Salvador that can be used by future researchers to monitor changes in relation to global, regional, and local factors affecting coral reef ecosystem health.

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