

Gulf and Caribbean Research

Volume 14 | Issue 2

January 2003

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Recommended Citation

Appeldoorn, R., A. Friedlander, J. Nowlis, P. Usseglio and A. Mitchell-Chui. 2003. Habitat Connectivity in Reef Fish Communities and Marine Reserve Design in Old Providence-Santa Catalina, Colombia. *Gulf and Caribbean Research* 14 (2): 61-77.
Retrieved from <https://aquila.usm.edu/gcr/vol14/iss2/5>
DOI: <https://doi.org/10.18785/gcr.1402.05>

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HABITAT CONNECTIVITY IN REEF FISH COMMUNITIES AND MARINE RESERVE DESIGN IN OLD PROVIDENCE-SANTA CATALINA, COLOMBIA

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ABSTRACT On the insular platform of Old Providence/Santa Catalina, Colombia, we compared nearshore lagoonal patch reefs to those on the northern bank distant from the islands to determine the importance of habitat connectivity to fish community structure. Nearshore patch reefs had greater proximity to mangrove, seagrass and rocky shore habitats, and they had significantly more individuals. Nearshore reefs also tended to have a greater total biomass, more species, a higher proportion of predators of mobile invertebrates and small fishes, and a lower proportion of herbivores. Biomass of snappers and grunts at nearshore sites was four times greater compared to bank sites, and was correlated with the amount of seagrass and sand/rubble habitat within 500 m of each patch reef. We also compared length-frequency distributions and abundances of grunts and snappers among all sites (deep and shallow forereefs, patch reefs and deep and shallow leeward slopes). The results were consistent with ontogenetic migrations from shallow sites, primarily seagrass and mangrove habitats, to deeper sites and to those further out on the bank. The evidence suggests that species differed in both distance and direction of dispersal, which may be affected by the abundance and distribution of preferred habitats. Marine reserves near the islands should target nearshore nursery areas and patch reefs harboring species of limited dispersal capability. Reserves on the northern bank would protect spawners of those species showing the greatest dispersal capability.

INTRODUCTION

Coral reef fishes form diverse and complex communities in tropical and subtropical environments that support intensive extractive and non-extractive commercial activities, such as fishing and tourist-based scuba diving. No-take marine reserves are a management tool, applicable for resource enhancement or conservation, that serves to promote the maintenance of a system's ecological structure, integrity and stability (Bohnsack 1996). These goals are best achieved if habitats supporting all species, and all life-stages, are encompassed within the reserve system, either in large closed areas or within a series of smaller reserves networked through the movement of individuals. This requires knowledge of the habitat requirements of species through ontogeny and their dispersal capabilities and pathways.

Coral reef fishes are variable in their use of habitats and the extent of their movement. Tag-recapture studies indicate that many reef species, at least as adults, are strongly site-attached. Recaptures at the tagging location are characteristic of most studies (Bardach 1958, Moe 1966, 1967, Randall 1961, 1963, Springer and McErlean 1962, Parker 1990, Recksiek et al. 1991, Corless et al. 1997, Friedlander et al. 2002). Short-term

acoustic tagging studies have shown similar results (Holland et al. 1993, 1996, Tulevech and Recksiek 1994, Zeller 1997, Meyer et al. 2000, Stewart and Jones 2001)

Nevertheless, although generally site-attached, reef species will undertake movements or migrations at various spatiotemporal scales. Several processes are involved, including temporary migrations for feeding (Stark and Davis 1966, Randall 1963, Hobsen 1972, 1973, Ogden and Ziemann 1977, Baker 1992, Ogden and Quinn 1984, Fishelson et al. 1987, Holland et al. 1993, 1996, Tulevich and Recksiek 1994, Meyer et al. 2000, Nagelkerken et al. 2000b) or spawning (Burnett-Herkes 1975, Johannes 1978, Robertson 1983, Colin et al. 1987, Shapiro 1987, Myrberg et al. 1989, PDT 1990, Zeller 1998). Two important factors in determining how far fishes move are size and the tendency to form groups: larger fishes and those in groups tend to range over greater areas (Roberts and Polunin 1993).

Ontogenetic onshore-to-offshore habitat transitions among tropical reef fishes are less studied than migrations to and from a "residence" site, but are common in many important groups, including the most desirable commercial species, e.g., snappers and groupers (Parish 1987 and references therein; see also references in Williams 1991). Typically, evidence for such habitat transi-

tions is based on differences in the size distributions of individuals across a shelf, with larger individuals found progressively offshore (e.g., Smale 1988, Rooker 1995, Dennis 1992a). Similar inferences can be made when species have specific known, near-shore settlement or nursery areas (e.g., McFarland 1979, Quinn and Kojis 1985, Rutherford et al. 1989a,b, Dennis et al. 1991, Dennis 1992b, Rooker 1995, Sheaves 1995, Lindeman and Snyder 1999). Detailed studies show these migrations often consist of distinct spatial separation in settlement areas, nursery areas, juvenile and adult feeding areas, and adult spawning areas (Eggleston 1995, Appeldoorn et al. 1997, Light and Jones 1997, Lindeman 1997, Lindeman et al. 1998, 2000, Eggleston et al. 1998, Nagelkerken et al. 2000a,c). These studies have demonstrated patterns of habitat use in some species, while growth studies coupled with site-specific size-frequency distributions can give an indication of the timing of habitat transitions and the potential distances of travel. The distribution of necessary habitat and the temporal scale of investigation confound studies of reef fish movement, however (Appeldoorn et al. 1997, Appeldoorn 1998). A complete lack of understanding of how fish move (direction of displacement) in relation to habitat distributions, current flow, population density gradients, etc. prevents the development of robust principles concerning habitat linkages.

In this study, we compare the fish communities between nearshore and offshore lagoonal patch reefs. Our purpose is to examine the potential effect of habitat connectivity, i.e., the degree of flow of individuals across the seascape between different habitat patches, on the species composition and trophic structure of these communities. In particular, we concentrate on grunts (Haemulidae) and snappers (Lutjanidae). Both ontogenetic habitat shifts and feeding migrations occur in these families, making them likely candidates to demonstrate the effects of habitat connectivity. They also are important components of commercial and subsistence fisheries of the Greater Caribbean Basin. We determine whether differences in the proximity to surrounding and/or nearshore habitats (e.g., mangroves, shallow seagrass beds, shallow rocky shores) influences the fish communities found on these reefs by examining connectivity at two spatiotemporal scales. Daily connectivity between shelter and feeding habitats was examined by comparing the abundance of fishes feeding on soft-bottom benthic invertebrates to the extent of available, nearby feeding habitat. On a larger scale, we used length-frequencies distributions from various habitats across the insular platform to examine potential ontogenetic pathways and

dispersal capabilities from nearshore nursery areas to offshore reefs.

METHODS

Study Site

The insular platform containing the small islands of Old Providence and Santa Catalina (OP/SC) is approximately 10 x 30 km and is located in the western Caribbean (Figure 1). The islands occur on the southern half of the platform and occupy an area of 18 km². Due to the physical isolation and small population (4,140) of the islands, the platform is among the least environmentally degraded locations in the wider Caribbean region. Artisanal fishing is an important industry, but the primary targets are conch, spiny lobster, coastal pelagic fishes and deep-slope demersal fishes, with scuba used for the invertebrates and hook and line used for the fishes. As a consequence, the shallow reef fish communities are largely intact relative to other Caribbean locations. (Friedlander et al. in press).

A complete description of the habitats on the platform is given by Sanchez et al. (1998) and Friedlander et al. (in press). The windward edge of the platform has a 32-km long continuous barrier reef with a sinuous fore-reef terrace. The northern and southern ends of the barrier reef crest consist of spurs of *Millepora complanata*, with colonies of *Porites* spp. and *Agaricia* spp., with the zoanthid *Palythoa* and encrusting red algae being abundant. The middle portion consists of pinnacles up to 5 m tall, again with *Millepora* on the top and coral colonies and encrusting algae along the walls. The windward forereef consists of a low relief terrace sloping gently from 7–12 m down to 30–35 m and ending at an extensive sand platform.

The lagoon basin contains numerous patch reefs characterized by high coral cover and overall benthic species diversity. To the north are found ribbon-like and anastomosing (Diaz et al. 1997) systems of coral heads (*Montastraea* spp.). In the middle region, patch reefs are smaller, more isolated, less abundant and contain a diverse coral community and dense populations of soft corals and gorgonians. Coral and algal cover are highly variable among patch reefs. The lagoon basin is interrupted by two diagonal sand bars containing large numbers of shallow patch reefs. These patch reefs are differentially characterized by large coral heads, dead *Acropora palmata*, and plexaurid gorgonians. The leeward margin (leeward slope habitat) is characterized by a rich mixed coral/octocoral community that terminates in a drop-off (45°–70°) with black corals, aposymbiotic

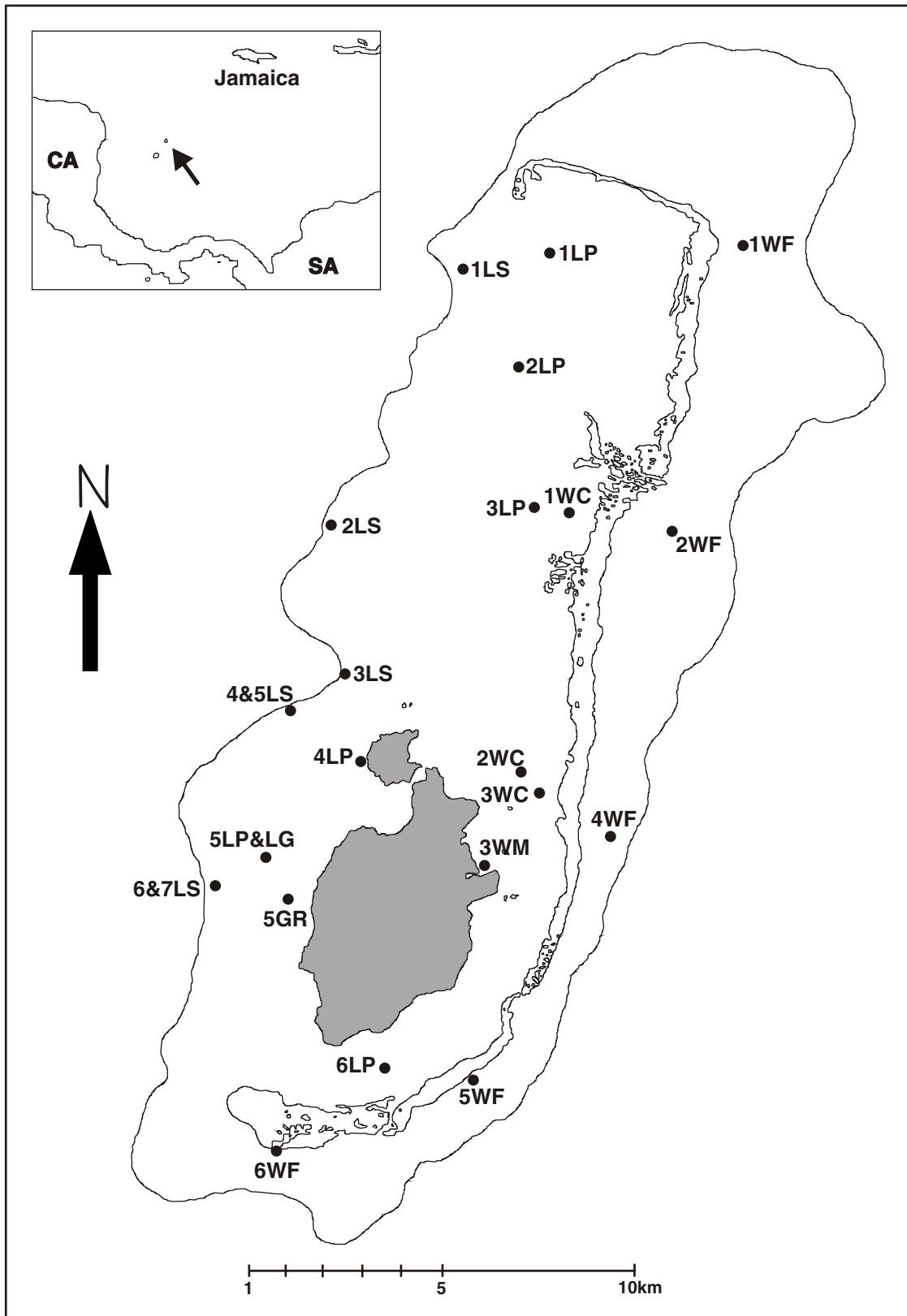


Figure 1. Sampling sites on the Old Providence/Santa Catalina platform. Islands are in gray. Outer solid line is the 100 m depth contour. Inner solid line represents the barrier reef. WF = windward forereef, LP = lagoonal patch reefs, LS = leeward slope, WC = windward crest, WM = windward mangroves, LG = lagoonal gorgonian, and GR = grass beds. In the inset: SA = South America, CA = Central America.

octocorals (ellisellids) and plate corals, typical of deep-water reef slopes (i.e., Sanchez 1999).

Seagrass beds, mangroves, and rocky shores border much of the islands' coast. There are two principal areas of shallow seagrass and mangroves: a small area found between the two islands and a large extent within the McBean Lagoon National Park on the northwest coast of Old Providence.

Sampling Strategy

A stratified sampling strategy was employed to incorporate various aspects of the geomorphological, environmental, and oceanographic conditions of the platform. The location of the islands on the insular platform, combined with a strong westward current flowing over the eastern barrier reef, effectively divides the platform into a southern portion in close proximity to the islands, and a northern bank with little influence from the distant islands. Depth and degree of wave exposure have been shown to be major factors affecting soft coral community composition and distribution around Old Providence (Sanchez et al. 1998). Therefore, sampling was stratified into bank and nearshore strata and additionally stratified into windward, leeward, and lagoonal locations. Sampling sites were located within two bank and two nearshore sampling swaths across the platform.

The fish fauna was characterized using visual census along measured strip-transects of 25 x 4 m for a total of 100 m² per transect. Strip-transects were chosen over point count methodologies because there is no clear indication that one method is superior to another (Bortone et al. 1989, Samoilys 1992) and because some habitats (e.g., mangroves) are not amenable to point-counts. Two of the divers identified all fishes within each transect. A third diver sampled a similar transect but only enumerated snappers, groupers and grunts to increase the sample size within these groups. Because of currents, diver safety and the need to maintain similar depths among replicates, divers ran their transects parallel, with approximately 4–5 m separating transects. After completing each transect, divers continued swimming in the same direction for approximately 5 m before starting the next transect. The total number of transects at each site was variable depending upon depth, current, and total fish abundance. However, all analyses except for length-frequency distributions were based on mean abundance over all transects per site. Each fish observed within a transect was identified to species, enumerated, and its total length (*TL*) classified into a 5-cm length class. Live wet weight, *W*, of all fishes recorded in all censuses was estimated from the visually estimated *TL* using the rela-

tion $W = a(TL)^b$. Values of the fitting parameters *a* and *b* for each species were derived from Bohnsack et al. (1986) and the FishBase web site (<http://fishbase.org/>). In the cases where length-weight information did not exist for a given species, the parameters from similar bodied congeners were used. Each species was classified into one of six trophic guilds following data in Dennis (1992a), Nagelkerken et al. (2000b), and Sierra et al. (2001): herbivore, mobile invertebrates, mobile invertebrates/piscivore, piscivore, sessile invertebrates, and plankton.

We calculated species diversity using the Shannon-Weaver Diversity Index (Ludwig and Reynolds 1988): $H' = -\sum(p_i \ln p_i)$, where p_i is the proportion of all individuals counted that were of species *i*. The evenness component of diversity was expressed as: $J = H'/\ln(S)$, where *S* is the total number of species present (Pielou, 1977).

We first examined whether the number and type of surrounding habitats, or proximity to nearshore habitats affects fish community structure by comparing the fish fauna at the bank and nearshore lagoonal patch. These habitats were spatially isolated, had a high diversity and abundance of fishes and had the highest number of replicate sites. Fish assemblage characteristics among bank and nearshore sites were compared using One-Way Analysis of Variance ($\alpha = 0.05$). Individuals and biomass were log-transformed for statistical analysis and back transformed for data presentation purposes. Data on proportion of biomass within feeding guilds were arcsine transformed prior to analysis.

A georeferenced habitat map for the OP/SC platform (INVEMAR, unpublished) was used to examine the number, and amount (area) of habitat types within 500 m and 1,000 m of the lagoonal patch reef sampling sites. Also obtained were the minimum distances from each sampling site to each of the different habitat types. To be consistent with the stratified sampling protocol, habitat types on the map were combined to form the following habitat types: Windward Forereef, Windward Crest, Lagoon Patch Reef, Lagoon Gorgonians, Lagoon Basin, Seagrass, Mangrove, Land, and Leeward Slope. Results from both fish assemblages and benthic communities suggest that this categorization of habitat types was ecologically relevant (Friedlander et al. in press). Seagrass habitats were further divided into those shallower or deeper than 3 m to differentiate potential nursery areas (Lindeman 1997, Lindeman et al. 1998, Nagelkerken et al. 2000a). Additionally, hard bottom less than 3 m depth (= shoals) was also designated for the same reason. All calculations were made using a Geographic Information System.

The biomass of grunts and snappers at the lagoonal patch reefs were each compared to the estimated available feeding grounds in the surrounding area. Seagrass beds and sand/rubble plains represent important feeding habitats for grunts and moderate sized snappers. Areas for these habitats were combined and their association to grunt and snapper biomass was examined using linear regression. The lagoon basin habitat, which consists mostly of coarse, loose and bioturbated sand, was not included because it is relatively poor in associated benthic invertebrate fauna.

The length frequency distributions of grunts and snappers were compared among all sites sampled across the OP/SC platform (Figure 1) to determine if there were shifts in the range and modal values indicative of ontogenetic migration from settlement and or nursery areas to adult habitats, and to determine if there were limits in the direction or distance of such migrations. For this analysis, data from all transects were used, so total sample sizes are affected by the number of transects conducted at each site. However, the examination of shifts in the distributions are based on the relative (%) length frequency within each site, not the absolute number, and each distribution will be more accurately represented the larger the number of individuals included in the sample. For this reason, only well represented species from these families are included in the analysis.

RESULTS

Analysis of Patch Reef Communities

The habitat characteristics of each sampling site were described by Friedlander et al. (in press) and are summarized in Table 1. Significant differences ($P < 0.05$) between nearshore and bank patch reefs were found, with nearshore sites having lower rugosity and higher percent sediment cover. Nearshore sites were characterized by

having a greater number of different habitat types surrounding them within both 500 m and 1,000 m, but the differences were significant ($P = 0.05$) only for the latter, with nearshore sites having more than twice the number of different nearby habitat types (Table 2). No significant differences were observed in habitat diversity or evenness within either distance. Differences in distance to nearest habitat type between nearshore and bank patch reefs were significant (Table 3). Nearshore sites were significantly closer to deep and shallow seagrass, mangroves, land margins and lagoon gorgonians. These results highlight that nearshore patch reefs were characterized by lower structural complexity, higher sediment cover, proximity to a greater number of habitats, and were significantly closer to mangrove, seagrass and other nearshore nursery habitats.

Community characteristics of the fishes at bank and nearshore sites are given in Table 4. Despite having greater mean species richness and much greater biomass on average, nearshore sites were significantly different ($P < 0.05$) from bank sites only in having a greater number of individuals. In most cases, considering the low number of sites within each category, the power of the tests were quite low. There were suggestions that the trophic structure of the nearshore and bank sites differed, with nearshore sites on average having a greater proportion of biomass in the mobile invertebrate and mobile invertebrate/piscivore trophic groups and a smaller proportion within the herbivores (Table 5). However, none of these differences were statistically significant, again with very low power. Snappers (Lutjanidae) and grunts (Haemulidae) belong to the former trophic groups and were important components of the patch reef communities. At nearshore sites there was a greater (4x) mean weight of these two families and they comprised a greater percentage of the total community biomass (Table 4).

TABLE 1

Habitat characteristics of patch reefs sampled. * = mean of two surveys. † = statistically significant difference ($\alpha = 0.05$) between bank and nearshore sites. Gorg. = gorgonians. (From Friedlander et al., in press).

| Location | Map code | Depth (m) | Association | Rugosity† | Coral cover | Coral species | Gorg density | Gorg species | Algal cover | Sediment cover† | Sponge cover |
|----------------------------|----------|-----------|-------------|-----------|-------------|---------------|--------------|--------------|-------------|-----------------|--------------|
| North bank patch reefs | 1LP | 9.9 | Bank | 1.98 | 37.74 | 21 | 9.29 | 4 | 17.46 | 7.93 | 2.29 |
| North bank leeward patches | 2LP | 6.7 | Bank | 2.10 | 31.50 | 12 | 17.15 | 9 | 41.55 | 3.90 | 0.40 |
| South bank lagoon patches | 3LP | 8.4 | Bank | 2.09 | 24.07 | 18 | 1.39 | 7 | 52.24 | 2.73 | 0.63 |
| Morgan's Head* | 4LP | 5.9 | Nearshore | 1.66 | 17.85 | 15 | 7.53 | 8 | 48.95 | 22.50 | 1.30 |
| San Felipe's Shoal* | 5LP | 6.7 | Nearshore | 1.66 | 29.69 | 23 | 9.70 | 11 | 31.69 | 13.04 | 3.59 |
| Manta City | 6LP | 6.9 | Nearshore | 1.60 | 38.07 | 11 | 0.30 | 1 | 17.86 | 19.60 | 1.02 |

TABLE 2

Area (Ha) of habitats within a 500-m and 1000-m radius of sampled patch reefs.

| Patch Reef | Habitat Type | | | | | | | | | |
|--|--------------|-------------------|-------------------|-----------------|----------------|----------------|-------|------|----------------|---------------|
| | Lagoon Basin | Lagoon Patch Reef | Lagoon Gorgonians | Sand and Rubble | Seagrass < 3 m | Seagrass > 3 m | Shoal | Land | Windward Crest | Leeward Slope |
| <i>Area of Habitats within 500 m</i> | | | | | | | | | | |
| 1LP | 36.5 | 41.6 | | | | | | | | |
| 2LP | 10.4 | 31.5 | | 14.4 | | | | | | 21.8 |
| 3LP | 63.8 | 14.3 | | | | | | | | |
| 4LP | 13.4 | 2.2 | | 1.5 | 39.6 | 3.8 | | 18.1 | | |
| 5LP | 41.5 | 0.3 | 32.8 | | 3.4 | | | | | |
| 6LP | 51.8 | 2.4 | | 23.9 | | | | | | |
| <i>Area of Habitats within 1,000 m</i> | | | | | | | | | | |
| 1LP | 154.7 | 154.4 | | | | | | | | 3.4 |
| 2LP | 82.7 | 76.4 | | 40.3 | | | | | | 113.0 |
| 3LP | 285.8 | 25.3 | | 1.4 | | | | | | |
| 4LP | 84.9 | 8.9 | 4.4 | 5.0 | 80.5 | 51.3 | 0.3 | 78.0 | | |
| 5LP | 138.1 | 20.0 | 87.1 | | 15.3 | 25.5 | | | | 25.6 |
| 6LP | 125.9 | 6.9 | | 136.2 | 33.0 | 2.1 | | 0.2 | 8.1 | |

Significant relationships were found between the biomass of grunts and snappers and the amount of soft-bottom feeding habitat within 500 m of each site (Figure 2). For areas within 1000 m (Figure 3), only the relationship with grunt biomass was statistically significant.

Analysis of Length-Frequency Distributions

French grunt, *Haemulon flavolineatum*. French grunt was the most commonly occurring species, being found at all but two sites near the central portion of the barrier reef (4WF, 3WC). Highest abundances were found at Morgan's Head (4LP) and San Felipe Shoal (5LP), and at two foreereef aggregations (1WF, 6WF). However, rea-

TABLE 3

Mean distance (meters) from bank and nearshore patch reefs to the nearest patch of each habitat type. SD = standard deviation, ns = not significant, s = significant.

| Habitat Type | Bank (N = 3) | | Nearshore (N = 3) | | Significance ($\alpha = 0.05$) |
|--------------------|--------------|-------|-------------------|-------|----------------------------------|
| | Mean | SD | Mean | SD | |
| Lagoon Basin | 22 | 38 | 109 | 189 | ns |
| Sand and Rubble | 758 | 591 | 569 | 882 | ns |
| Lagoon Patch Reef | 8 | 14 | 284 | 162 | ns |
| Lagoon Gorgonians | 11,360 | 2,949 | 1,162 | 1,511 | s |
| Land | 9,780 | 3,216 | 919 | 724 | s |
| Mangrove | 10,617 | 3,263 | 1,904 | 821 | s |
| Seagrass <3m depth | 9,656 | 3,148 | 429 | 380 | s |
| Seagrass >3 depth | 9,492 | 3,092 | 475 | 247 | s |
| Shoals | 6,164 | 3,226 | 3,780 | 1,848 | ns |
| Windward Crest | 1,674 | 409 | 3,511 | 2,641 | ns |
| Windward Foreereef | 2,976 | 1,177 | 4,581 | 2,932 | ns |
| Leeward Slope | 1,372 | 1,542 | 2,250 | 2,269 | ns |

TABLE 4

Comparison (mean and standard deviation) of fish assemblage characteristics from 25 x 4-m belt transects at nearshore and bank patch reef sites. Biomass is in grams. P-value records the level of statistical significance; Power gives the power of the test assuming $\alpha = 0.05$.

| | Bank (N = 3) | | Nearshore (N = 3) | | P-value | Power |
|-----------------------|--------------|----------|-------------------|----------|---------|-------|
| | Mean | Std.Dev. | Mean | Std.Dev. | | |
| Species Diversity | 2.43 | | 2.513 | | | |
| Species Evenness | 0.793 | | 0.777 | | | |
| Species Richness | 21.71 | 0.193 | 25.873 | 4.868 | 0.213 | 0.133 |
| Number of Individuals | 112 | 19 | 190 | 29 | 0.017 | 0.809 |
| Total Biomass | 3700 | 1246 | 6453 | 3166 | 0.234 | 0.117 |
| Grunt Biomass | 437 | 156 | 1524 | 711 | 0.038 | 0.584 |
| Snapper Biomass | 313 | 44 | 1340 | 602 | 0.001 | 1.000 |

sonable numbers were observed at most other sites (Table 6). Sites in which individuals were observed in the smallest length class (0–5 cm) were near the island; the mangrove prop root habitat at McBean Lagoon (3WM) serves as a nursery area, but not to the extent observed in some other species. Nearshore sites also tended to show a broad range of sizes; note that while no small juveniles were observed within the transects at Morgan's Head, several schools of newly settled French grunts were observed at the site. There was a progressive increase in length away from the islands toward the outer bank.

White grunt, *Haemulon plumieri*. All patch reefs had white grunts, but the abundance at Morgan's Head (4LP) was 3 to 5 times greater than observed at other sites. Overall, white grunts were found at all but one forereef site (4WF), two leeward slope sites (1LS, 3LS) and the mangrove habitat at McBean Lagoon (3WM). Length-frequency distributions suggest an ontogenetic shift from nearshore sites to more distant sites (Table 7). Dominance by large juveniles and small adults in the 10–15 and 15–20 length classes was only found at Morgan's

Head (4LP) and Manta City (6LP), both nearshore patch reefs. At all other sites larger adults (length classes from 20 to 35 cm) were found.

Blue striped grunt, *Haemulon sciurus*. Although small individuals were seen at several sites, the data suggested that two areas in particular were important nursery areas, harboring small juveniles in the size range of 5 to 20 cm: Morgan's Head (4LP) and the mangrove prop root habitat at McBean Lagoon (3WM). Abundances at these sites were also one to two orders of magnitude greater than other sites, with the exception of a large aggregation of adults observed at the northernmost forereef site (1WF). A distinct shift in size frequency distributions was observed at other sites, including other patch reefs, forereef sites and nearshore leeside slope sites. Data in Table 8 suggest an ontogenetic movement of blue striped grunts from the nursery areas to areas west and south around the island and north on to the bank. Abundances at patch reef sites out on the bank were an order of magnitude less than at nearshore patch reefs. No individuals were observed at bank leeside slope sites.

TABLE 5

Percentage of total biomass by trophic guild for fish assemblages at nearshore and bank patch reefs. Herb. = herbivores, Mobile Inverts. = mobile invertebrate feeders, MI/P = mobile invertebrate and piscivore feeders, Pisc. = piscivores, Sessile Inverts. = sessile invertebrate feeders, and Plank. = planktivores

| | Trophic Group | | | | | |
|-----------|---------------|-----------------|------|-------|------------------|--------|
| | Herb. | Mobile Inverts. | MI/P | Pisc. | Sessile Inverts. | Plank. |
| Bank | 54.5 | 27.4 | 6.4 | 1.7 | 6.9 | 3.1 |
| Nearshore | 23.8 | 42.8 | 19.5 | 2.6 | 3.1 | 8.3 |

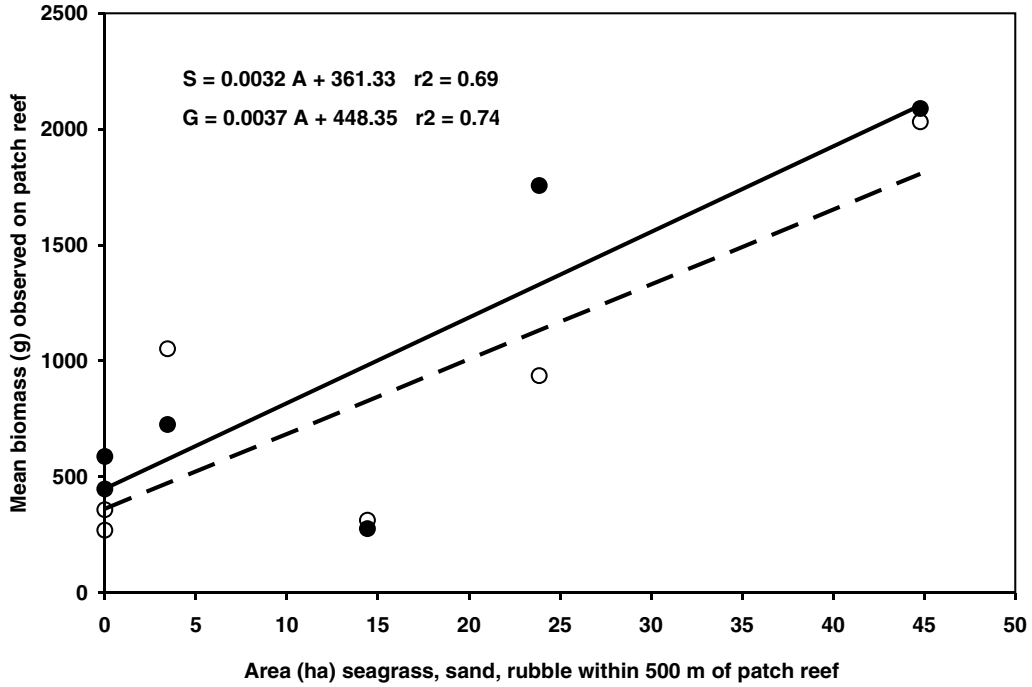


Figure 2. Relationship between the mean biomass of grunts (G; filled circles, solid line) and snappers (S; open circles, dashed line) observed in 24 x 4-m belt transects at each patch reef and the area of seagrass and sand/rubble habitat within 500 m of the sampling sites.

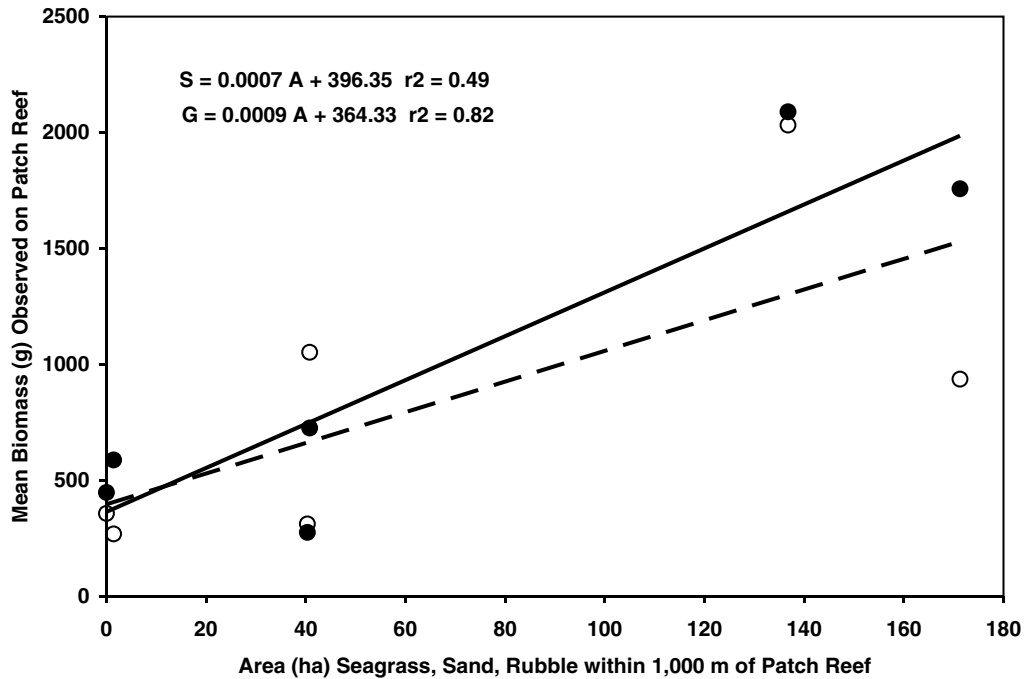


Figure 3. Relationship between the mean biomass of grunts (G; filled circles, solid line) and snappers (S; open circles, dashed line) observed in 24 x 4-m belt transects at each patch reef and the area of seagrass and sand/rubble habitat within 1,000 m of the sampling sites.

HABITAT CONNECTIVITY

TABLE 6

Percent length-frequency distributions for French grunt, *Haemulon flavolineatum*. N = sample size. See Figure 1 for site locations.

| Sampling Site | Site Code | Length Class (cm TL) | | | | | N | |
|-------------------------------------|-----------|----------------------|------|-------|-------|-------|----|-------|
| | | 0-5 | 5-10 | 10-15 | 15-20 | 20-25 | | 25-30 |
| North bank windward forereef | 1WF | | | 51 | 44 | 5 | 61 | |
| North bank leeward slope | 1LS | | | 67 | 11 | 22 | 9 | |
| North bank patch reefs | 1LP | | 5 | 42 | 32 | 21 | 19 | |
| North bank leeward patches | 2LP | | | 41 | 35 | 24 | 17 | |
| South bank forereef | 3WF | | | | 100 | | 6 | |
| South bank leeward slope | 2LS | | | | 33 | 67 | 3 | |
| South bank lagoon patches | 3LP | | 4 | 54 | 38 | 4 | 26 | |
| South bank <i>Acropora</i> forereef | 2WF | | 33 | 33 | 33 | | 6 | |
| South bank crest | 1WC | | 4 | 48 | 40 | 8 | 25 | |
| Inactive pinnacles | 2WC | 11 | 37 | 32 | 11 | 5 | 5 | 19 |
| Blue Hole | 3LS | | | 33 | 67 | | 6 | |
| Morgan's Head | 4LP | | | 25 | 48 | 27 | 60 | |
| McBean Lagoon | 3WM | | 100 | | | | 22 | |
| San Felipe Shoal | 5LP | 30 | 19 | 23 | 15 | 11 | 2 | 111 |
| Cathedral | 6LS, 7LS | 45 | 18 | | 18 | 18 | | 11 |
| Felipe's Place | 4LS | | | | 50 | 50 | | 2 |
| Manta City | 6LP | | | | 86 | 14 | | 7 |
| Manchineel Bay forereef | 5WF | | | 75 | 25 | | | 4 |
| South forereef | 6WF | | | 33 | 67 | | | 144 |

TABLE 7

Percent length-frequency distributions for white grunt, *Haemulon plumieri*. N = sample size. See Figure 1 for site locations.

| Sampling Site | Site Code | Length Class (cm TL) | | | | | | | N | |
|-------------------------------------|-----------|----------------------|------|-------|-------|-------|-------|-------|-----|-------|
| | | 0-5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-30 | 30-35 | | 35-40 |
| North bank windward forereef | 1WF | | | | | 83 | 17 | | | 6 |
| North bank patch reefs | 1LP | | | | 7 | 67 | 20 | 7 | | 15 |
| North bank leeward patches | 2LP | | | | | 75 | 25 | | | 4 |
| South bank forereef | 3WF | | | | | | 100 | | | 1 |
| South bank leeward slope | 2LS | | | | | 71 | 29 | | | 7 |
| South bank lagoon patches | 3LP | | | | 7 | 71 | 14 | 7 | | 14 |
| South bank <i>Acropora</i> forereef | 2WF | | | | 17 | 67 | 17 | | | 6 |
| Active pinnacles | 3WC | | | | | 100 | | | | 2 |
| Inactive pinnacles | 2WC | | | | 50 | | 50 | | | 2 |
| Morgan's Head | 4LP | | | 25 | 54 | 19 | 2 | | | 81 |
| San Felipe's Shoal | 5LP | | | | 30 | 52 | 19 | | | 27 |
| Cathedral | 6LS, 7LS | | | | 9 | 64 | 27 | | | 11 |
| Felipe's Place | 4LS | | | | | 50 | | 50 | | 2 |
| Manta City | 6LP | | | 60 | 20 | 20 | | | | 10 |
| Manchineel Bay forereef | 5WF | | | | 4 | 96 | | | | 26 |
| South forereef | 6WF | | | | | | | | 100 | 1 |

TABLE 8

Percent length-frequency distributions for blue striped grunt, *Haemulon sciurus*. *N* = sample size. See Figure 1 for site locations.

| Sampling Site | Site Code | Length Class (cm TL) | | | | | | | <i>N</i> |
|-------------------------------------|-----------|----------------------|------|-------|-------|-------|-------|-------|----------|
| | | 0–5 | 5–10 | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | |
| North bank windward forereef | 1WF | | | | 20 | 27 | 53 | | 96 |
| North bank patch reefs | 1LP | | | | 50 | | 50 | | 2 |
| North bank leeward patches | 2LP | | | | | | 100 | | 2 |
| South bank forereef | 3WF | | | | | | 100 | | 1 |
| South bank lagoon patches | 3LP | | | | | 44 | 44 | 11 | 9 |
| South bank <i>Acropora</i> forereef | 2WF | | | | | 100 | | | 1 |
| South bank crest | 1WC | | | | | 17 | 83 | | 6 |
| Active pinnacles | 3WC | | | | | 100 | | | 1 |
| Inactive pinnacles | 2WC | | | | | 25 | 75 | | 4 |
| Morgans's Head | 4LP | 53 | 24 | 18 | 5 | | 0 | | 357 |
| San Felipe's Shoal | 5LP | 14 | | | 57 | 27 | 3 | | 37 |
| Cathedral | 6LS, 7LS | | | 33 | | 67 | | | 3 |
| Felipe's Place shelf | 5LS | | | | | 100 | | | 12 |
| McBean Lagoon | 3WM | 29 | 47 | 25 | | | | | 824 |
| Manta City | 6LP | 7 | | 7 | 62 | 21 | 3 | | 29 |
| Manchineel Bay forereef | 5WF | | | | | | 100 | | 1 |

Yellowtail snapper, *Ocyurus chrysurus*. Length-frequency distributions for yellowtail snapper are given in Table 9. The greatest abundance of yellowtails occurred at San Felipe's Shoal (5LP). Lengths spanned the 0 to 30-cm length classes, but 75% fell within the 20–25 cm length class. A similarly broad length range, but with

much lower abundance, was observed at Manta City (6LP). In general, there is an increase in length distributions running from the northern nearshore site of Morgan's Head (4LP) progressively north on to the bank, terminating at the northernmost forereef site (1WF). In similar fashion but with greater abundances, length distribu-

TABLE 9

Percent length-frequency distributions for yellowtail snapper, *Ocyurus chrysurus*. *N* = sample size. See Figure 1 for site locations.

| Sampling Site | Site Code | Length Class (cm TL) | | | | | | | | <i>N</i> |
|------------------------------|-----------|----------------------|------|-------|-------|-------|-------|-------|-------|----------|
| | | 0–5 | 5–10 | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | 35–40 | |
| North bank windward forereef | 1WF | | | | 45 | 45 | 9 | | | 11 |
| North bank patch reefs | 1LP | | | | 40 | 60 | | | | 10 |
| North bank leeward patches | 2LP | | | | 44 | 56 | | | | 9 |
| South bank lagoon patches | 3LP | | | 60 | 20 | 20 | | | | 5 |
| South bank crest | 1WC | | | 50 | 50 | | | | | 2 |
| Morgan's Head | 4LP | | | 56 | 44 | | | | | 9 |
| San Felipe Shoal | 5LP | 1 | 2 | 2 | 11 | 72 | 11 | | | 83 |
| Cathedral | 6LS, 7LS | | | | 44 | 38 | 6 | 13 | | 16 |
| Felipe's Place shelf | 5LS | | | | 50 | 50 | | | | 2 |
| Felipe's Place | 4LS | | | | 17 | 33 | 17 | 33 | | 12 |
| Blue Hole | 3LS | | | | | 47 | 53 | | | 15 |
| Manta City | 6LP | | 50 | | 10 | | 20 | | 20 | 10 |
| Manchineel Bay forereef | 5WF | | 100 | | | | | | | 1 |

TABLE 10

Percent length-frequency distributions for schoolmaster snapper, *Lutjanus apodus*. *N* = sample size. See Figure 1 for site locations.

| Sampling Site | Site Code | Length Class (cm TL) | | | | | | | | <i>N</i> |
|------------------------------|-----------|----------------------|------|-------|-------|-------|-------|-------|-------|----------|
| | | 0–5 | 5–10 | 10–15 | 15–20 | 20–25 | 25–30 | 30–35 | 35–40 | |
| North bank windward forereef | 1WF | | | | | 100 | | | | 2 |
| North bank leeward patches | 2LP | | | | | | | 100 | | 1 |
| South bank lagoon patches | 3LP | | 42 | 17 | | 17 | 25 | | | 12 |
| South bank crest | 1WC | | | | 17 | 50 | 17 | 17 | | 6 |
| Active pinnacles | 3WC | | | | 100 | | | | | 2 |
| Inactive pinnacles | 2WC | | | 57 | 14 | 14 | 14 | | | 7 |
| Blue Hole | 3LS | | | 25 | | 50 | 25 | | | 4 |
| Morgan's Head | 4LP | | | 29 | 30 | 25 | 3 | 11 | 1 | 79 |
| McBean Lagoon | 3WM | 1 | 25 | 35 | 38 | 1 | | | | 216 |
| San Felipe's Shoal | 5LP | | 35 | 6 | 6 | 18 | 18 | 12 | 6 | 17 |
| Cathedral | 6LS, 7LS | | | | | 100 | | | | 1 |
| Felipe's Place | 4LS | | | | | 48 | 52 | | | 23 |
| Felipe's Place shelf | 5LS | | | | | | 100 | | | 1 |
| Manta City | 6LP | | | | | 67 | 33 | | | 3 |
| McBean Lagoon | 3WM | 1 | 25 | 35 | 38 | 1 | | | | 216 |

tions generally increase from Morgan's Head (4LP) and San Felipe's Shoal (5LP) to the leeward slope sites near the island; no yellowtail snappers were observed at leeward slope sites on the bank.

Schoolmaster snapper, *Lutjanus apodus*. Schoolmasters were observed at all sites near the island. The majority was found within the mangrove prop root habitat at McBean Lagoon (3WM), predominately spanning the length classes from 5–20 cm (Table 10). Large numbers were also found at Morgan's Head (4LP) ranging from 10–40 cm in length, but dominant abundance fell within the 10–25 cm length classes. The data suggest an ontogenetic shift in length distributions, where at the leeward slope habitat (Felipe's Place, 4LS) only large individuals were observed. On the bank, schoolmasters were observed at two of the three patch reef sites, but abundance decreased with increasing distance from the island. However, two individuals were found at the northernmost forereef site (1WF). Small juveniles (5–10 cm length class) were also observed at two of the patch reef sites (San Felipe's Shoal (5LP) nearshore, and at the south bank lagoon patches (3LP)), but abundances were an order of magnitude lower than observed at McBean Lagoon (3WM).

Gray snapper, *Lutjanus griseus*. Gray snapper were observed at only two sites, both immediately adjacent to land and shallow seagrass and mangrove habitats in particular. Over 400 individuals were counted in the mangrove prop root habitat at McBean Lagoon (3WM), with most falling within the 10–15 and 15–20 cm length classes. At Morgan's Head (4LP), 25 individuals were recorded spanning all length classes from 5 to 40 cm. The majority was greater than 25 cm in length.

Mutton snapper, *Lutjanus anilis*. An abundance of small juveniles, mostly in the 10–15 cm length class, was found in the mangrove prop roots of McBean Lagoon (3WM). No individuals larger than 20cm were recorded there, indicating this habitat served as a nursery area. Scattered individuals, much larger in size (25–50 cm TL) were found at all nearshore patch reefs and at Blue Hole (3LS), a near island leeward deep slope site. Only one individual was found on the bank, at the South Bank Crest site (1WC) about half way up the bank.

Mahogany snapper, *Lutjanus mahogoni*. On the bank, mahogany snappers were only found at the patch reef habitats and only in low numbers. Near the island they were found at all patch reefs plus the deep leeward slope habitats. Abundances at the nearshore patch reefs were 2–10 times greater than observed on the bank. The

smallest juveniles (5–10 cm length class) were only observed near the island at San Felipe Shoal (5LP).

Dog snapper, *Lutjanus jocu*. Within the mangrove prop roots at McBean Lagoon (3WM), 123 individuals were recorded spanning lengths from 5–25 cm, with 68% in the 5–10 cm length class and another 25% in the 10–15 cm size class. Only three other dog snappers were recorded, all from nearshore patch reefs: two from San Felipe Shoal (5LP) and one from Morgan's Head (4LP). These were larger than observed in McBean Lagoon, ranging from 20 to 40 cm in length.

DISCUSSION

We examined the differences in habitats surrounding both nearshore and bank patch reefs to determine if any habitat differences affected the fish communities observed on the reefs. We found no differences in the shortest distance between these patch reefs and lagoon basin, patch reef and sand/rubble habitats. The sites themselves were patch reefs and by definition their contextual setting was lagoon basin and sand/rubble, and these habitats were all in close proximity. No differences were also noted in the shortest distance to windward crest, windward forereef and leeward slope habitats (means typically 1–3 km). Again, this comes from the definition of these sites as patch reefs, which must occupy a middle position on the platform relative to the windward and leeward margins. Large differences between nearshore and bank patch reefs were found in the minimum distance to those habitats associated within shallow areas near the island (mangrove, shallow seagrass beds, land = rocky shoreline). Mean distances from nearshore patch reefs to

these habitats were less than 1 km while comparable distances from bank sites were 9–10 km. The spatial scale of the differences observed between bank and nearshore patch reefs in the shortest distance to near-island habitats also explains the significantly greater number of different habitats found within 1,000 m of nearshore patch reefs. Large differences between nearshore and bank patch reefs were also found for the shortest distance to deep seagrass and lagoon gorgonian habitats. While these habitats are not necessarily limited to near-island areas, on the OP/SC platform they occur only in the southern portion and are hence closer to the island sites. No differences were observed for shoals (= broad extent of shallow bedrock), but this habitat occurs in only a few locations on the platform.

The above differences in the habitat landscape around nearshore and bank patch reefs did not lead to significant differences in fish community structure and function except for number of individuals. This result contrasts with those of Friedlander et al. (in press) who found significantly greater biomass over all nearshore sites on the OP/SC platform compared to all bank sites. However, with the low number of replicates in the present study the power of these tests were all quite low, so we may not have detected any differences between the two sets of patch reefs, if they in fact existed. Additionally, there are other factors that may mask the effect of habitat variability at landscape scales. For example, rugosity was significantly greater at bank sites, and rugosity has been correlated to species abundance and diversity (e.g., Luckhurst and Luckhurst 1978, Roberts and Ormond 1987, McCormick 1994, Friedlander and Parrish 1998), yet mean biomass, species richness and diversity tended to be higher at nearshore sites. Despite the lack of obvi-

TABLE 11

Settlement and/or nursery habitats for snappers and grunts as summarized from the literature. Sources: Rooker 1995, Lindeman 1997, Lindeman and Snyder 1999, Lindeman et al. 1998, 2000, Nagelkerken et al. 2000a,c, Hill 2001.

| Species | Settlement/Nursery Habitat |
|-------------------------------|--|
| <i>Lutjanus griseus</i> | Obligate to seagrass (preferred) and mangroves |
| <i>Lutjanus anilis</i> | Estuarine dependent, shallow seagrass and mangrove |
| <i>Lutjanus mahogoni</i> | Seagrass or shallow reef |
| <i>Lutjanus apodus</i> | Shallow seagrass, then mangrove, uses shallow reef opportunistically |
| <i>Lutjanus jocu</i> | Estuarine dependent, shallow seagrass |
| <i>Ocyurus chrysurus</i> | Seagrass and mangrove preferred |
| <i>Haemulon flavolineatum</i> | Seagrass and hardbottom, very opportunistic settler |
| <i>Haemulon plumieri</i> | Seagrass, some mangrove and hardbottom |
| <i>Haemulon sciurus</i> | Seagrass, then mangrove, some hardbottom |

ous differences in overall fish community structure, differences were observed at the family level, with nearshore patch reefs having a much greater biomass of both snappers and groupers than bank sites. Given that these are two of the most abundant families (20% by biomass at the bank sites and 40% at the nearshore sites), these differences do indeed constitute an important difference between nearshore and bank patch reef communities.

The species-specific examinations of spatial variations in length-frequency distributions support the idea that some near-island habitats act as nursery areas. Generally, the observed patterns of abundance of small juveniles followed known patterns of habitat use for these species (Table 11). In this study, shallow seagrass beds were not surveyed. However, the prop root habitat (and associated shallow seagrass bed) at McBean Lagoon (3WM) appeared to serve as a nursery area for several species. The only additional extent of this type of habitat was located in the waters between the two islands, not far from Morgan's Head (4LP)(Figure 1). For some species (e.g., gray and dog snappers) our results indicated little to no dispersal away from these habitats, while for others (e.g., mutton and mahogany snappers) the data suggested there was moderate dispersal (although the wider distribution of mahogany snapper may be due to opportunistic settlement (Table 11) in shallow reef environments. Lack of dispersal among these species would be an obvious contributing factor to the differences in the biomass of snappers among nearshore and bank patch reefs. Generally, the grunts as a whole showed wide distributions. In particular, the French grunt had by far the widest distribution on the platform, and it is reported to be the most opportunistic species with respect to settlement and nursery habitats (Table 11). Nevertheless, higher abundances of juvenile grunts for all species were still found at nearshore sites, indicating either preferential settlement or greater juvenile survival in these areas, which would contribute to the biomass differences of grunts between nearshore and bank reefs. The tendency for nursery areas to be preferentially located at nearshore sites was strongest for bluestriped grunts, with large abundances of juveniles in the mangrove lagoon and at Morgan's Head (4LP) and moderate dispersal to other nearshore patch reefs and the leeward slope. For all species for which the data suggested a large or moderate degree of dispersal from nearshore habitats, the apparent dispersal was always greater toward the lee side. This was particularly apparent in species such as bluestriped grunt and schoolmaster snapper, for which dominant abundance was observed for juveniles in McBean Lagoon on

the windward side of the island, yet leeward patch reefs and slope environments showed greater abundances of adults.

The relationship of grunt and snapper biomass to the extent of surrounding seagrass and sand/rubble habitats suggests that the distribution of these species is limited by available habitat associated with feeding. Grunts are primarily soft-bottom feeders although large individuals are capable of feeding in hard bottom areas (Dennis 1992a), while many snappers, although piscivorous when large, feed on benthic invertebrates as juveniles and young adults (Randall 1967, Rooker 1995, Nagelkerken et al. 2000b). Studies of movement in the white grunt (Tulevich and Recksiek 1994) and on the distribution of French grunts relative to seagrass habitats (Kendall et al. in press) indicate that the range of foraging in these species is limited to about 300 m, which is consistent with the spatial scale for the observed correlations.

The differences in biomass of grunts and snappers between nearshore and bank patch reefs can be explained within the context of habitat connectivity, and this can be done at the scales of both feeding and ontogenetic migrations. On the smaller scale, bank patch reefs appear to lack sufficient nearby soft-bottom feeding habitats to support an abundance of grunts and snappers. This alone may explain their lower abundances at bank sites. On the other hand, substantial differences in species diversity, richness and biomass were found at sites other than patch reefs (Friedlander et al. in press), and examination of the length-frequency distributions suggests that dispersal to all bank habitats may be limited to some extent. For example, significantly greater overall fish abundance and biomass at nearshore deep leeward slope habitats (Friedlander et al. in press) would not be expected on the basis of connectivity to soft-bottom habitats, as these are quite limited at all leeward slope sites. Rather, the inference is that ontogenetic migration does have limits of its own, i.e., distance alone may be important in limiting the extent of dispersal. However, it is likely that the effect of distance is modulated by the distribution and abundance of available habitat and by factors affecting the choice of migration direction. This is also indicated by the fact that the distribution patterns vary markedly among species, suggesting they are responding to differential habitat preferences.

We hypothesize three mechanisms by which habitat distribution could limit the extent of ontogenetic migration. If adult habitat is not limiting, nearshore areas may merely fill up first, leaving little incentive to seek habitats further away. This is certainly conceivable within the OP/SC platform, where shallow, island-associated settle-

ment/nursery areas are located only within the southern portion. The distribution of desired habitat may also affect the direction of migration. That abundances of those species suggested to undertake significant ontogenetic migration tend to be greater on the leeward side of the platform may indicate that these migrations are not simply movement directly offshore at the nearest point. The orientation of the OP/SC platform perpendicular to the prevailing east-west current may also play a significant role as a habitat variable. The apparent limitation of feeding areas at bank patch reefs (Figures 2,3, Table 2) points to a third mechanism. Lack of local connectivity between reef and feeding habitats may result in a bottleneck in the distribution of essential habitat that results in a reduction in subsequent dispersal, i.e., the limited feeding areas at bank patch reefs may restrict the number of mid-sized individuals to the extent that there are too few to subsequently migrate out to other habitats further out on the bank.

The Corporation for the Sustainable Development of the Archipelago of San Andres, Old Providence and Santa Catalina (CORALINA), Colombia, is currently developing a regional system of multiple-use marine reserves to improve the conservation and sustainable use of the marine resources of the archipelago. In an initial phase of this project, a group of scientists focused on the islands of Old Providence and Santa Catalina and incorporated biological and sociological information on the marine resources of the islands to help develop preliminary marine reserve zoning options (Friedlander et al. in press). Based on apparent differences between bank and nearshore sites overall, this group recommended that separate marine reserve sites be designated at both near island and outer bank locations. The present study supports this recommendation and provides a mechanistic justification. Two of the most basic tenets of marine reserve network design are that all habitats be represented and that the resulting network be self-sustaining (Ballantine 1997a,b). Here, habitat serves as a proxy measure for community composition and structure, with the real goal being to preserve all distinct biological assemblages. In the case of OP/SC, the differences among island and bank sites are subtle but significant enough to consider them as being distinct, especially with respect to species of limited dispersal from shallow water settlement and nursery areas. Thus, both island and bank sites are worthy of protection. The requirement of self-sustainability addresses squarely the issue of habitat connectivity. Biological communities can only be self-sustaining if the habitats supporting them are also intact and protected. In this case, preservation of the OP/SC

patch reef communities requires that reserves be large enough to include surrounding soft-bottom habitats, at least out to 500 m in the case of grunts and snappers. The potential for ontogenetic connectivity among habitats puts further constraints on reserve design. The important role that the mangrove, shallow seagrass and shallow rocky shoreline habitats play as settlement and nursery areas mandates that the critical areas for these habitats (McBean Lagoon (4LP), Morgan's Head (3WM), and the area between Old Providence and Santa Catalina) be designated as marine reserves. These sites serve not only the near island communities, but also those out on the bank. Lastly, the length-frequency distributions suggest that, for some species, patch reefs are serving as links to other habitats, such as the leeward deep slope. Thus, it is imperative that complete linkages be protected. The most obvious such corridor in OP/SC is the westward connection from the islands, through such highly diverse sites as Morgan's Head and San Felipe Shoal (5LP), to the slope environments such as Felipe's Place. Similar arguments can be made for preserving corridors on the windward side, noting in particular the aggregations of adult grunts observed at several forereef sites (Tables 6,8, and Friedlander et al. in press). Because of their high fecundity, large adults are particularly important contributors to the spawning stock.

ACKNOWLEDGMENTS

The authors wish to acknowledge the financial and logistical assistance of The Ocean Conservancy and CORALINA. We especially thank June Marine Mow, Marion Howard and Elizabeth Taylor from CORALINA, and Cheri Recchia from The Ocean Conservancy, for their assistance in arranging and hosting field visits. Juan Sánchez, Claudia McCormick, and Sonia Bejarano were also instrumental in collecting field data.

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