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ASSESSING 50-YEAR CHANGE IN BAHAMIAN REEF FISH ASSEMBLAGES: EVIDENCE FOR COMMUNITY RESPONSE TO RECENT DISTURBANCE?

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ABSTRACT

The Caribbean has experienced long-term declines in coral reef habitat. Research on the effect of habitat degradation has emphasized the importance of time since disturbance on reef fish response. We examined whether reef fish community structure was retained over a 50-yr period off the coast of New Providence Island, The Bahamas, in areas with increased dead coral and algal cover. Using baseline data from 1955 to 1973, we resurveyed four localities in 2006 using comparable methodology to assess historical and current reef fish community structure. We did not find evidence for changes in diversity through time; however, our results were suggestive of several patterns that should be further explored. Analysis of similarity (ANOSIM) showed that both shallow and deep sites have experienced change through time. A general pattern of relative increase was seen in the herbivore trophic group, as well as the squirrelfishes, parrotfishes, and, qualitatively, the wrasses, which may be explained by an increase in algal cover and/or a decrease in predation pressure. Planktivores, primarily cardinalfishes, showed a trend towards decreased relative abundance. Overall, the results were consistent with a hypothesis that reef fish assemblages around New Providence Island are responding to the effects of relatively recent (< 10 yrs) coral loss. Distinct differences were also found between depths above and below 6 m, irrespective of time or site. These areas should be continually monitored to track long-term effects, particularly given the proliferation of the invasive lionfish, *Pterois volitans* (Linnaeus, 1758), subsequent to the time frame examined in this study.

Caribbean coral reefs have been in decline for decades (Gardner et al. 2003, 2005, Alvarez-Filip et al. 2009). The causes of these declines are both natural and anthropogenic, and include hurricanes, coral disease, mass mortality of invertebrate algal grazers, pollution, physical habitat destruction, nutrient run-off, and warming water temperatures (Hughes 1994, Aronson and Precht 2001, Gardner et al. 2003, Burke and Maidens 2004, Otis et al. 2004, Gardner et al. 2005, Wilson et al. 2006, Hoegh-Guldberg et al. 2007). A question of particular interest in coral reef community ecology is how reef fish communities are affected by such widespread coral habitat degradation (Jones and Syms 1998, Bellwood et al. 2006, Wilson et al. 2009). Species that require live coral for survival, such as obligate corallivores, have shown significant declines in abundance and, in some instances, have gone locally extinct following coral loss (Berumen and Pratchett 2006, Pratchett et al. 2006); however, studies addressing whether fish community structure and species diversity are maintained in the face of such loss and degradation have yielded disparate

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answers (Walsh 1983, Knowlton 1992, Halford et al. 2004, Garpe et al. 2006, Wilson et al. 2009, McCormick et al. 2010).

The disparities in results from empirical studies reflect the complexities of examining the relationship between reef fish community structure (and/or diversity) and coral loss. A lack of change in species diversity despite massive loss of coral habitat has been recorded in multiple studies, primarily from sites in the Indian Ocean and the Great Barrier Reef (e.g., McClanahan et al. 2002, Sheppard et al. 2002, Spalding and Jarvis 2002, Bellwood et al. 2006). Interpretation of the apparent lack of effect of coral loss on fish communities, however, is complicated by numerous factors. For instance, a focus simply on diversity measures may miss important changes in community composition, such as the loss or dominance of particular trophic groups (e.g., Bellwood et al. 2006, Cheal et al. 2008). Furthermore, as emphasized by Bellwood et al. (2006), Garpe et al. (2006), and Graham et al. (2006, 2007), a time lag between coral death and the subsequent effect on the surrounding reef fish community may obscure the true impact of disturbance, such as bleaching, in studies with data collected immediately following such an event. In particular, a pattern that may denote an early stage of reef fish community response to coral loss is an increase in herbivorous species that corresponds to an increase in algal cover following (or perhaps causing) loss of live coral (Sheppard et al. 2002, Cheal et al. 2008, Wilson et al. 2009).

Whether or not coral decline is followed by physical collapse has been suggested as a primary determinant of the surrounding fish community's response. If structural complexity is retained, there is evidence that even with large reductions in live coral cover, reef fishes do not show changes in diversity. On the other hand, loss of live coral, accompanied by diminished structural complexity of the reef, may be expected to have larger associated changes in reef fish communities (Luckhurst and Luckhurst 1978a, Syms and Jones 2000, Almany 2004, Garpe et al. 2006, Wilson et al. 2008). Dead coral stands may remain intact for several years, and possibly decades in the case of non-branching species, but if they do not recover, they will eventually collapse due to erosion resulting from both biological (bioeroders) and physical (e.g., storms, wave action) sources (Glynn 1997, Garpe et al. 2006, Pratchett et al. 2008, 2009). Furthermore, the duration of a disturbance, ranging from a single event (storm, disease outbreak) to ongoing stressors (repeated storms, temperature increase, pollution), affects the time frame and/or possibility of coral recovery (Connell 1997, Berumen and Pratchett 2006, Wakeford et al. 2008). Studies examining the effect of coral loss must therefore take into consideration the timing and duration of habitat disturbance events when interpreting the results of fish community structure analyses.

To assess whether there is evidence for change in reef fish community structure in a region with known coral depletion (Pandolfi et al. 2003, Sealey 2004, Jaap et al. 2008), we revisited four sites near New Providence Island, The Bahamas, that were sampled by J Böhlke and C Chaplin of the Academy of Natural Sciences (ANSP) between 1955 and 1973 (Böhlke and Chaplin 1968). New Providence Island, home to the Bahamian capital, Nassau, is a popular tourist destination, and has consequently experienced rapid development and population growth, particularly along its coastline (Sealey 2004). Although quantitative assessments of coral cover around New Providence Island pre-1970 are lacking, examinations of photographs yielded estimates of 30%–40% in many areas of The Bahamas, and a coral survey contemporaneous with our study estimated coral cover at 2%–20% with a rugosity index of

1.20–1.83 at our study sites (Jaap et al. 2008), suggesting declines in coral cover have occurred over the time frame encompassed by our study. In addition, the recollections of one of us (GWC), a participant in many of the original collections, about the habitat at three of the four historical sites are consistent with an increase in both dead coral and algal cover, but little change in the coral architecture (online Appendix Text S1). The historic Böhlke and Chaplin collections, therefore, provide an important set of baseline reef fish community structure and distribution data that is quite rare in marine systems.

Following a similar sampling regime with an ichthyocide-based methodology, we collected fishes from reefs matching four historical sites with the aim of examining temporal changes in the fish assemblages of New Providence Island coral reefs. Despite the decline in coral cover at the four study sites, the retention of physical structure through time leads us to expect minimal changes in species richness (Bellwood et al. 2006, Graham et al. 2006). Further, because the Caribbean lacks the obligate corallivore species that characterize many regions of other tropical oceans (Cole et al. 2008), we have no a priori expectations regarding the decreased representation or loss of particular reef species. The increase in algal cover (Jaap et al. 2008, online Appendix Text S1) and the documented reduction of predators in the Caribbean (Stallings 2009, Ward-Paige et al. 2010) may, however, have effects on the reef fish community assemblages, with possible increases in taxa released from predation pressure and/or changes in the dominant trophic groups (e.g., Sheppard et al. 2002, Bellwood et al. 2006, Cheal et al. 2008).

Methods

Locality Choice and Site Descriptions

The sites resurveyed in July and November, 2006, near New Providence Island, The Bahamas, were chosen by reference to the historical Böhlke and Chaplin field notes (deposited at the ANSP) and the recollections of one of us (GWC), who participated in many of the original and in the two 2006 surveys (Chaplin 2006). The main criteria for site selection were: accessibility from New Providence Island, confidence in historical locality/reef identification (often difficult to obtain from field notes prior to GPS coordinate availability), and, if possible, the availability of multiple historical replicate sampling events. Based on these criteria, four historical sites were selected for resurvey: Lyford Cay/Clifton Point, Delaporte Point, North/Long Cay, and Green Cay (Fig. 1, Table 1). Historically, these sites were sampled at a single depth range, but in 2006, additional insight into community structure was explored by collecting fishes on reefs in the area at three depth ranges, categorized into "shallow" (< 6 m), "mid" (6 to < 12 m), and "deep" (12–18 m). A description of the 2006 sites comparable to those sampled historically (LC1, DP1, NL1, and GC3) follows below.

Lyford Cay.—The LC1 site was located 0.6 km due west from the tip of Lyford Cay (Simms Point) at the western end of New Providence Island; an isolated patch reef oval in shape (ca. 600 m^2), surrounded by sand. Depths ranged from 2.5 to 5.5 m. Wave surge was partly buffered by barrier and submerged bank reefs to the north and by New Providence Island to the east. Stacks of dead staghorn coral (*Acropora cervicornis*, see online Apendix Table S1 for species authorities) were visible at the base of the reef, but no live specimens were evident. The Böhlke and Chaplin Field Notes (May 8, 1956) described this site as an "isolated coral head west of tip of Lyford Cay, west end of New Providence … surrounded by sand, ca. ¼ mi from shore."

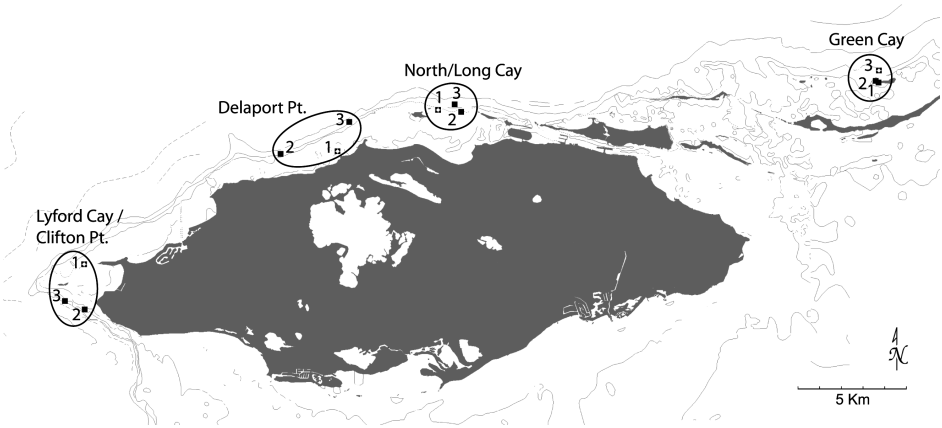

Figure 1. Map of sampling sites off the coast of New Providence Island, The Bahamas. Historical sampling sites are open boxes. Details and coordinates are listed in Table 1.

Delaporte Point.—The DP1 site was ~1 km west from the tip of Delaporte Point and 290 m from the closest land point to the south. This patch reef was in the shape of a "U" opening toward shore (sampling was within U). The inner base of the patch reef was ~4 m deep and was located behind an extensive barrier reef that may increase water retention times and buffer storm surge. The Böhlke and Chaplin field notes (April 11, 1955; with sketch) described this site as a "sandy bottomed 'U' in a large coral head offshore and just a bit west (ca. ¼ mi) of Delaporte Point … surrounded on three sides by large composite coral head with attendant gorgonians, etc." One of us (GWC) remembers this site as having good coral cover and rugosity, with little algae (found only at the shallow rocky top) and a variety of coral species, including small stands of elkhorn (online Appendix Text S1).

North/Long Cay.—The NL1 site was in closest proximity to the Bahamian capital and population center of Nassau, 4.6 km west-northwest from the western tip of Paradise Island, ~500 m northeast from the eastern most tip of North Cay. This forereef location extended from the seaward crest edge to the trough of a shallow spur and groove reef (depths from 2 to 4 m). This site had tidally strong north–south currents and is exposed to storm surge from the north. Baiting by resort dive/snorkel boat operators may occur in the area. The Böhlke and Chaplin Field Notes (August 5, 1955) describe the sites as "North edge of coral head between North Cay and small cay just off Long Cay … coral with many caves and crevices, sea fans, whips, etc." This site was also described as having healthy coral, although lacking branching coral, and with less coral and algal cover than Delaporte Point (online Appendix Text S1).

Green Cay.—The GC3 site was an isolated patch reef located 10.1 km northeast of New Providence Island, or ca. 360 m north of the west end of Green Cay. The reef was nearly circular (~35 m across), rising near vertically from a depth of 14.5 m to within 6.0 m of the surface. The Green Cay reef was surrounded by a wide area of white sand and was located inshore of extensive submerged, shelf-edge reefs. This site was deeper and more exposed than others, because reefs to the north are deeper and do not provide an effective barrier to currents and storm surge. The Böhlke and Chaplin Field Notes (May 14, 1959) described the site as a "Deep head north of Green Cay about ¼ mi north-northwest of the cays … fine white sand around an isolated coral head which rose at its highest point about ⅔ the distance from the bottom to the surface." One of us (GWC) remembers this site as having a diversity of healthy corals, including branching species (although lacking *Acropora* spp.), and a diversity of invertebrate macrofauna. Brown algae were common only in the caves at the base of the reef (online Appendix Text S1).

Table 1. Sampling site locations, depths, and replicates included in analysis. Site numbers correspond to those in Fig. 1. Year of collection is indicated for the historical sampling events. If sampling events were excluded from final analyses (see text), the total number of original sampling events is indicated in parentheses. + indicates historical sampling events that were excluded. * The "deep" Green Cay site (GC3) crosses the "deep" and "mid" depth zones as the reef rises from 14.5 to 6 m.

					Data from 2006		
Locality	Coordinates	Depth	Historical replicates	2006 replicates	Rugosity index	Coral cover (%)	Algal cover (%)
Lyford Cay (LC)							
1	25°01´45.2″N 77°33´35.8″W	4.8 m (shallow)	1 [(2) 1956, 1968+]	1	1.49	2.99	57.10
2	25°00´38.1″N 77°33´33.7″W	8.5 m (mid)	0	1	1.22	1.81	81.68
3	25°00´50.7″N 77°34´6.7″W	17.0 m (deep)	0	1	1.15	1.23	59.80
Delaport Point (DP)							
1	25°04´34.7″N 77°26´37.9″W	4.5 m (shallow)	3 [1955]	1 (2)	1.47	2.04	28.26
2	25°04´28.3″N 77°28´12.6″W	8.1 m (mid)	0	1 (2)	1.44	11.95	51.85
3	25°05´16.8″N 77°26´18.3″W	14.0 m (deep)	0	1 (2)	1.20	0.65	2.83
North/Long Cay (NL)							
1	25°05´34.6″N 77°23´54″W	5.5 m (shallow)	1 [1955]	1	N/A	N/A	N/A
2	25°05´32.4″N 77°23´15.2″W	9.0 (mid)	0	1 (2)	N/A	N/A	N/A
3	25°05´42.3″N 77°23´25″W	15.2 m (deep)	0	1	N/A	N/A	N/A
Green Cay (GC)							
1	25°06´17″N 77°11´49.3″W	4.5 m (shallow)	0	1 (2)	1.77	20.56	32.22
2	25°06´17.5″N 77°11´51.4″W	7.0 m (mid)	0	1 (2)	1.83	6.29	72.06
3*	25°06´32.8″N 77°11´44.9″W	14.5 m (deep)	6 [(8) 1956, 1957, 1959, 1969, 1972+, 1973+]	1 (2)	1.43	12.98	73.19

Despite an increase in both algal cover and dead coral at all of our study sites, relative to the historical time period, the reefs at these sites have retained their physical structure (GWC, online Appendix Text S1).

Fish Collection and Identification

Fishes were collected using the ichthyocide rotenone, in a slurry containing 3 gal of 5% Chemfish Regular, 3 cups (~710 ml) of Joy Ultra Concentrated detergent, and seawater up to a final volume of 15 gal. This mixture was released at depth around each site, making sure that it penetrated crevices and under ledges. Similar protocols were implemented for the historical collections. The effects of rotenone were apparent after 15 min, and were monitored for 2 hrs with three to eight SCUBA divers searching the treated area and collecting affected fishes in nets. On the surface, when possible, tissue samples were taken from a representative of as many species as possible and placed in 95% ethanol for future molecular analyses. The collected fishes were then fixed in a 10% buffered formaldehyde solution and washed in water prior to transportation back to the ANSP for identification.

The FAO guide to species identification for the western central Atlantic (Carpenter 2003) and Böhlke and Chaplin's classic work (Böhlke and Chaplin 1968, 1993) were used as primary

sources for specimen identification, with continuous reference to the historical collections at the ANSP. In addition, more recent literature was consulted for a number of groups, including brotulas (Bythitidae, Møller et al. 2005), cardinalfishes (*Phaeoptyx*, Baldwin et al. 2008), gobies (*Coryphopterus*, Baldwin et al. 2009), and scaly blennies (*Starksia*, Williams and Mounts 2003). Material in historic collections was reassessed in cases of identification uncertainty, to update taxonomy, or to verify and maintain taxonomic consistency across time periods. All specimens have been accessioned and catalogued into the ANSP Ichthyology collection.

Data Analysis

Raw data used in this study appear in the online Appendix Table S1. Prior to data analysis, historical and 2006 field notes were examined for details of sampling protocols and success, and the resulting species lists. Sampling events that were reported in field notes to be compromised (e.g., "poor kill") were excluded from further analysis because they were not deemed as representative of either absolute or relative species abundance and could further bias results by indicating low species richness. Since the study objectives were to compare reef fish assemblages, species considered not generally coral reef dependent (e.g., pelagic carangids) were excluded from the dataset. "Non-reef" species were identified based on Choat and Bellwood (1991) and our own knowledge of reef fish ecology. We were particularly sensitive to species that are potentially less vulnerable to our sampling method, such as jawfishes and flounders that generally live in the sand. In addition, species that were only collected at a single time in a single location were excluded so as not to bias the results based on extraordinarily rare collections. Taxa identified only to "sp." (due to developmental stage, specimen size, and/or quality) were also excluded, because it is unlikely that these unidentified individuals are unique from the species in the dataset, and therefore should not be treated as unique taxa in the data analysis. Only non-reef species were excluded from family and trophic group relative abundance calculations. For each site, standard diversity indices, including S (number of species) and H´ (Shannon diversity index), and relative abundances by trophic level and family were calculated with PRIMER 6 (Clarke and Gorley 2006). Following Paddack et al. (2009), species were categorized into one of six trophic groups (herbivore, planktivore, omnivore, invertivore, carnivore, piscivore) based on information from Randall (1966, 1967), Luckhurst and Luckhurst (1978b), Randall and Böhlke (1981), Randall (1983), Lieske and Myers (1996), Dominici-Arosemena and Wolff (2005), and Paddack et al. (2009), followed by FishBase (Froese and Pauly 2010), as necessary.

Rarefaction Curves.—To compare species richness across current and historical time periods, species accumulation curves scaled to the number of individuals (Gotelli and Colwell 2001) were calculated using the analytical Mao Tao method (Colwell et al. 2004) in EstimateS (Colwell 2009). Because the 2006 expeditions sampled at depths not visited in the past, rarefaction curves were produced for both the entire 2006 dataset and a reduced 2006 dataset that included only the sites directly comparable to the historical data (LC1, DP1, NL1, GC3).

Multivariate Analyses.—Multivariate analyses were conducted to examine fish assemblage structure by depth, location, and time of collection (Clarke and Warwick 2001, Clarke and Gorley 2006). Pairwise community composition similarities across the 23 samples were visualized using multi-dimensional scaling (MDS) and hierarchical cluster analyses (Clarke 1993). Raw abundances were standardized and fourth-root transformed prior to calculation of Bray-Curtis coefficients (Bray and Curtis 1957) to down-weight the very abundant species so both rare and mid-abundance species could also influence the similarity between sites. Analysis of similarity (ANOSIM) was used to test for differences in community composition between depths (shallow vs deep), sites within depths (shallow, deep), and time periods within depths (shallow, deep). ANOSIM significance is based on the calculation of an R statistic, which measures the difference between sampling groups (e.g., shallow and deep depths) based on the idea that a true difference between groups would be reflected by larger differences in species composition among sites between the groups than among sites within the groups.

An R value of 0 indicates no difference between groups, while an R value of 1 indicates all between-group differences are larger than all within-group differences (Clarke and Warwick 2001). The results of the ANOSIM analyses should be treated with caution, however, because one of the shallow sites (GC1) and three of the deep sites (LC3, DP3, NL3) were not sampled historically. Similarity percentage (SIMPER) analysis (Clarke 1993) was used to explore which species potentially contributed to differences identified from the ANOSIM results. For these analyses, the mid sites were excluded as this depth range was not sampled historically. The MDS, cluster, and ANOSIM analyses were also conducted on a dataset that included the "rare" and "non-reef" species to examine any possible effects of their exclusion; this yielded essentially identical results (data not shown).

Univariate Analyses.—To test for differences in the relative abundance of each trophic group and family between the historical and 2006 time periods, we conducted two-sample t-tests (Student's or Welch's) or Wilcoxon rank sum tests, depending on whether assumptions of normality and equal variances were met, using the "stats" package in R (R Development Core Team 2008). When examining family relative abundance, we combined all families with a mean relative abundance of < 1% across sites into an "Other" category.

Additional Considerations.—From the literature and through examination of historical and 2006 collections, it was clear that numerous taxa are in need of revision, were inconsistently identified, and/or different life history stages complicated identifications. For an increased level of conservatism, multivariate analyses were repeated on a condensed dataset where problematic species were grouped at higher taxonomic levels. The species in the following genera were grouped as a single taxon, with the number of taxa in parentheses: *Apogon* spp. (12), *Phaeoptyx* spp. (4), *Coryphopterus* spp. (only *Coryphopterus dicrus*, *Coryphopterus eidolon*, and *Coryphopterus glaucofraenum* grouped), *Elacatinus* spp. (2), *Starksia* spp. (4), *Stegastes* spp. (7), *Scarus* spp. (4), *Sparisoma* spp. (5), *Hypoplectrus* spp. (4), and *Enneanectes* spp. (5). In addition, all 10 collected species in the family Bythitidae were grouped as Bythitidae spp. in the more conservative analyses.

Results

Collection Details and Species Accumulation Curves

The four sites were historically sampled a total of 14 times between 1955 and 1973, and 19 times in 2006. Three sites had replicate sampling events in the historical period [LC1 (two replicates), DP1 (three replicates), and GC3 (eight replicates)] and seven sites had replicate samples in 2006 [DP1, DP2, DP3, NL2, GC1, GC2, and GC3 (all with two replicates)]. Due to sampling issues, however, three historical and seven 2006 sampling events were excluded from further analysis (Table 1, online Appendix Table S2), which included one historical replicate at LC1, two historical replicates at GC3, and one of the replicates from each of the replicated 2006 sites. The raw historical data yielded 5348 individuals representing 203 species, while the raw 2006 data yielded 5423 individuals across 183 species (online Appendix, Table S1). Fifty-eight species were unique to the historical collections and 38 species were unique to the 2006 collections (online Appendix Table S3), with 145 species shared across time periods. These numbers are slightly misleading, however, as only 15 of the unique historical species and 14 of the unique 2006 species were reef species collected on more than one occasion (online Appendix Table S3). Further, 24 of 27 unique reef species in the historical collections were from the deep Green Cay site that was sampled eight times between 1956 and 1973 (online Appendix Table S3). Similarly, 21 of 30 identified reef species only collected in 2006 included sites that were not sampled

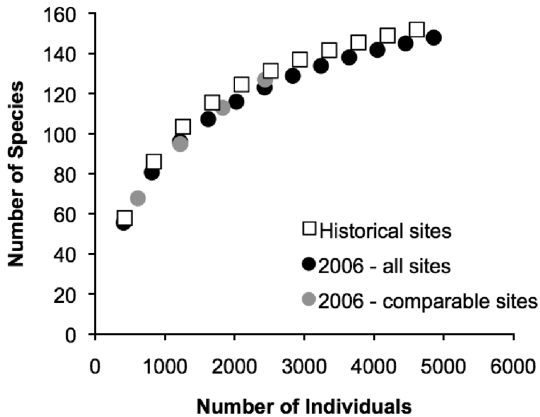

Figure 2. Fish species accumulation curves for the historical dataset (open squares), the entire 2006 dataset (black circles), and the 2006 sites directly comparable to the historical sites (gray circles).

historically (online Appendix Table S3). One species, caught only in 2006, is a particular standout: the lionfish (*Pterois volitans*), an introduced species native to the Indo-Pacific. An additional species of note is the saddle squirrelfish (*Sargocentron poco*), of which only a single specimen was ever collected in The Bahamas [at a deep Green Cay site (GC3)] through all of the Böhlke and Chaplin fieldwork. Three specimens of this species were collected in 2006—two from the deep Green Cay site and one additional from the mid-depth Lyford Cay locality (LC2).

Prior to multivariate and species diversity analyses, 79 taxa were removed from the dataset because they either were identified as "sp." (19 spp.), were not considered reef-dependent (17 spp.), were only collected at excluded sites (5 spp.), or were only collected at a single collecting event (38 spp., online Appendix Table S4). Taking these exclusions into consideration, the analyzed dataset included 9471 individuals across 165 species, where the historical dataset had 4614 individuals representing 152 species (17 unique) and the 2006 dataset had 4857 individuals representing 148 species (13 unique), leaving 135 shared species across the dataset.

Species accumulation curves of the collections grouped by time period (historical, 2006) are largely similar (Fig. 2, 95% confidence intervals not shown). The historical and 2006 dataset curves appear to approach an asymptote at ~150 species (Fig. 2). The similarity of the rarefaction curves provides confidence that the reefs were adequately sampled across time periods. On the other hand, the four directly comparable 2006 sites did not quite reach a species asymptote due to the smaller sample size; however, the shape of the curve matches that of the complete dataset.

Multivariate Analyses

The MDS plot, with a stress value of 0.16 (within the range of confidence, Clarke 1993), showed a pattern of sites clustering by depth (Fig. 3). Similarly, hierarchical agglomerative clustering yielded two major groups where the shallow sites generally clustered together separately from the combined mid and deep sites (online Appendix Fig. S1). ANOSIM tests of difference between sites within shallow and deep depths did not yield significant differences ($R = 0.24$, $P = 0.19$; $R = 0.47$, $P = 0.06$, respectively), which allowed us to group the sites for further analysis. Due to the lack

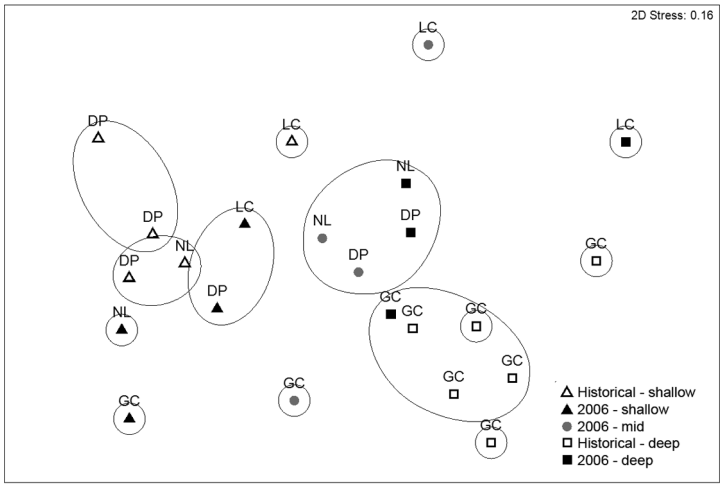

Figure 3. MDS plot of Bray-Curtis similarities of standardized, fourth-root-transformed fish abundance data across the historical and 2006 sites. Contour lines mark sites with 60% similarity of reef fish community composition.

of depth by site replication, the results should be treated with caution. This is particularly relevant at the deep sites where only a single site was sampled at a deep depth.

An ANOSIM test of difference in community structure between shallow and deep depths yielded a significant difference ($R = 0.74$, $P < 0.001$), which is consistent with the MDS and cluster plots (Fig. 3, online Appendix Fig. S1). SIMPER analysis did not reveal a clearly discriminating species or group of species between depths (shallow vs deep), as 48 species were required to account for 50% of the dissimilarity between depth ranges. The longjaw squirrelfish, *Neoniphon marianus*, which was primarily collected at deep sites, showed the highest ratio of $\bar{\delta}_i/\mathrm{SD}(\delta_i)$ at 2.94, but contributed only 1.64% of the total dissimilarity between depth zones. The second highest contributor to the difference was the whitestar cardinalfish, *Apogon lachneri*, which was also primarily found at deep sites, with $\bar{\delta}_i/\mathrm{SD}(\delta_i) = 2.84$, and a 1.69% contribution to total dissimilarity across depth. Rounding out the top five discriminating species were the blenny, *Ophioblennius macclurei* [$\bar{\delta}_i/\mathrm{SD}(\delta_i) = 2.29$, 1.53% contribution], collected only at shallow sites, the royal gramma, *Gramma loreto* [$\bar{\delta}_i/\mathrm{SD}(\delta_i) = 1.70$, 1.73% contribution], found primarily at deep sites, and the mimic blenny, *Labrisomus guppyi* [$\bar{\delta}_i/\mathrm{SD}(\delta_i) = 1.69$, 1.56% contribution], collected only at shallow sites.

Repeating the ANOSIM test between depths at the family level also yielded a significant difference between shallow and deep sites ($R = 0.46$, $P < 0.001$). SIMPER analysis showed that the five families with the highest $\bar{\delta}_i/\mathrm{SD}(\delta_i)$ (Bleniidae, Gobiidae, Grammatidae, Scorpaenidae, and Labrisomidae) explained over 20% of the total dissimilarity (details in online Appendix Table S7). Of these families, the blennies, gobies, and labrisomids had primarily shallow distributions, while the basslets and scorpaenids were collected primarily at deeper depths (online Appendix Table S7).

ANOSIM tests showed minimal, but significant, differences between time period collections from the shallow (Global $R = 0.31$, $P < 0.02$) and deep ($R = 0.44$, $P < 0.01$) depths. We caution over-interpretation of these results, given the general lack of replicates, the missing data for the shallow, historical GC1 site, and for three of the four deep, historical sites (LC3, DP3, NL3). We also note that the fish assemblage

Table 2. Sample size (N), number of species (S), Shannon diversity index (H´), and depth category for each site. Comparable historical and 2006 sites are grouped with historical sites highlighted in bold text. Sample site codes as in Table 1.

Site (mm/dd/yyyy)	N	S	H'	Depth
LC1 (11/12/2006)	516	63	3.25	shallow
LC1 (05/08/1956)	**160**	**43**	**3.43**	shallow
LC2 (11/11/2006)	112	30	3.47	mid
LC3 (11/10/2006)	116	34	3.05	deep
DP1 (11/12/2006)	442	64	3.52	shallow
DP1 (09/05/1955)	**346**	**59**	**3.43**	shallow
DP1 (07/27/1955)	**292**	**54**	**3.45**	shallow
DP1 (04/11/1955)	**132**	**44**	**2.81**	shallow
DP2 (11/13/2006)	752	65	3.13	mid
DP3 (11/14/2006)	251	52	3.56	deep
NL1 (07/14/2006)	466	59	3.19	shallow
NL1 (08/5/1955)	**279**	**64**	**3.53**	shallow
NL2 (11/09/2006)	177	53	3.33	mid
NL3 (07/13/2006)	185	48	3.59	deep
GC1 (11/16/2006)	372	52	3.29	shallow
GC2 (11/16/2006)	456	62	3.52	mid
GC3 (11/15/2006)	1012	85	3.62	deep
GC3 (05/07/1956)	**228**	**46**	**3.04**	deep
GC3 (05/12/1957)	**113**	**31**	**2.63**	deep
GC3 (07/21/1957)	**837**	**66**	**2.99**	deep
GC3 (05/14/1959)	**826**	**80**	**3.41**	deep
GC3 (11/14/1959)	**904**	**91**	**3.81**	deep
GC3 (08/27/1969)	**497**	**59**	**3.04**	deep

at the 2006 GC site was more similar to the historical GC assemblages compared with the 2006 NL and DP sites (Fig. 3). SIMPER results between time periods at the shallow and deep sites showed that 42 and 41 species, respectively, were required to explain 50% of the difference between time periods (online Appendix Tables S8, S9). At the shallow depth, of the top five discriminating species, the blackfin cardinal fish (*Astrapogon puncticulatus*) was predominantly collected during the historical collections, while the coralbrotula (*Ogilbia boehlkei*), marbled moray (*Uropterygius macularius*), longspine squirrelfish (*Holocentrus rufus*), and lofty triplefin (*Enneanectes altivelis*) were primarily collected in 2006 (details in online Appendix Table S8). At the deep sites, the top five discriminating species included the rock beauty angelfish (*Holacanthus tricolor*) which was found primarily in historical collections, and the redband parrotfish (*Sparisoma aurofrenatum*), harlequin basslet (*Serranus tigrinus*), longjaw squirrelfish (*N. marianus*), and longfin blenny (*Labrisomus haitiensis*), which were predominantly collected in 2006 (details in online Appendix Table S9).

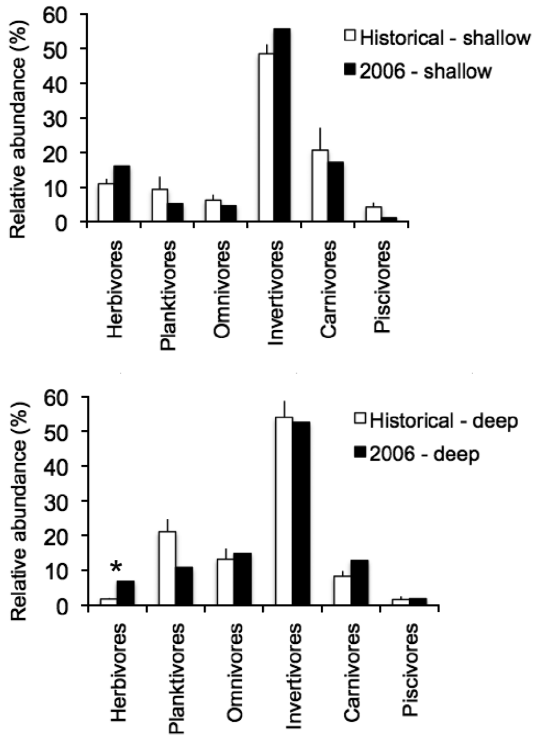

Figure 4. Relative abundance of trophic groups between historical and 2006 collections at shallow and deep sites. Bars represent standard error and * indicates significant result at $P < 0.05$ (Table 3).

Univariate Analyses

Sample size, species richness, and the Shannon diversity index for each site showed no clear pattern across time periods or depth (Table 2), supported by a lack of significant difference in mean H′ between historical and 2006 samples at shallow ($\bar{x}$ = 3.93, 4.04, respectively; t = 1.18, P = 0.28) and deep ($\bar{x}$ = 4.02, 3.92, respectively; t = −0.44, P = 0.67) depths. The relative abundance of herbivores increased between historical and 2006 collections at both shallow and deep sites (Fig. 4); however, this difference was only significant for the deep sites (W = −3.90, P = 0.03; Table 3). Further, although there was an apparent decrease in the relative abundance of planktivores between historical and 2006 time periods at both shallow and deep depths (Fig. 4), the differences were not statistically significant (Table 3). Similarly, there were few significant differences in family level relative abundances (Fig. 5): only squirrelfishes (holocentrids) at shallow (t = −5.03, P = 0.002) and parrotfishes (scarids) at deep (t = −3.46, P = 0.03) reefs increased significantly over time, although an increasing trend was seen in squirrelfishes, parrotfishes, and wrasses (labrids) at both shallow and deep depths (Fig. 5, Table 4).

Table 3. Tests for normality, equal variances, and equal means for trophic group relative abundance between time periods. + indicates violation of normality or equal variances assumption, ^ indicates Wilcoxin rank sum W statistic calculated, and * indicates significant differences between time periods (P < 0.05).

	Mean relative abundance (SD)		Shapiro-Wilks test W		Shapiro-Wilks test P		F test		t-test (Wilcoxin signed rank test^)	
Trophic group	Historial	2006	Historical	2006	Historical	2006	F	P	t (W^)	P
Shallow										
Herbivores	10.96 (3.19)	16.08 (7.08)	0.96	1.00	0.81	0.99	0.20	0.16	–1.46	0.19
Planktivores	9.38 (8.36)	5.22 (5.02)	0.86	0.91	0.23	0.50	2.77	0.43	0.87	0.41
Omnivores	6.19 (3.83)	4.65 (2.70)	0.90	0.96	0.41	0.78	2.00	0.59	0.68	0.52
Invertivores	48.53 (5.95)	55.67 (6.08)	0.97	0.90	0.86	0.44	0.96	0.93	–1.77	0.12
Carnivores	20.70 (14.47)	17.13 (4.85)	0.89	0.97	0.35	0.82	8.91	0.10	0.47	0.66
Piscivores	4.25 (2.79)	1.25 (0.88)	0.94	0.94	0.65	0.68	10.07	0.09	2.05	0.08
Deep										
Herbivores	1.76 (0.71)	6.87 (2.56)	0.89	0.92	0.34	0.53	0.08	0.02+	–3.90	0.03*
Planktivores	21.19 (8.67)	10.91 (6.41)	0.88	0.90	0.27	0.42	1.83	0.66	2.01	0.08
Omnivores	13.19 (7.78)	14.95 (9.89)	0.89	0.82	0.29	0.14	0.62	0.60	–0.32	0.76
Invertivores	53.98 (11.52)	52.55 (12.63)	0.92	0.88	0.54	0.33	0.83	0.80	0.19	0.86
Carnivores	8.28 (3.97)	12.85 (2.14)	0.96	0.95	0.85	0.73	3.46	0.34	–2.08	0.07
Piscivores	1.61 (2.19)	1.87 (1.23)	0.64	0.82	< 0.01+	0.14	N/A	N/A	6.50^	0.29

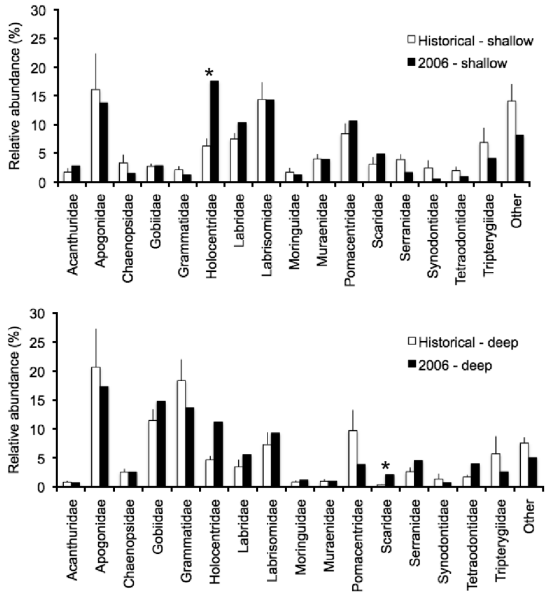

Figure 5. Relative abundance of families between historical and 2006 collections at shallow and deep sites. Families with a mean of < 1% relative abundance across sites were grouped into "Other." Bars represent standard error and * indicates significant result at $P < 0.05$ (Table 4).

Discussion

The large Böhlke and Chaplin collections of coral reef fishes from The Bahamas made between 1955 and 1973 provide a rare opportunity to compare historical and current reef fish community structure. In 2006, we resurveyed four of the Böhlke and Chaplin localities off New Providence Island using comparable collecting methods. Habitat surveys (Jaap et al. 2008) and the recollections of one of us (GWC) revealed an increase in algal cover and dead coral, but with little change in the physical reef structure from the 1950s through 2006. This finding, in conjunction with the results from our comparative community analyses, suggests that the fish assemblages of the reefs around New Providence Island are at an early stage (< 10 yrs) of response to habitat disturbance. We also found a partitioning of species by depth that is consistent with that from other Caribbean regions.

Comparisons Between Historical and Current Species Assemblages

Long-term degradation of Caribbean coral reefs has been widely reported (e.g., Gardner et al. 2003, 2005, Hughes et al. 2003, Hoegh-Guldberg et al. 2007, Alvarez-Filip et al. 2009, Paddack et al. 2009). A coral habitat survey conducted along with our reef fish surveys in July 2006 found that coral cover at our focal sites had been diminished to 2%–20% from pre-1970 levels that exceeded 30%–40% in many areas of The Bahamas (Jaap et al. 2008). Personal observations of one of us (GWC) also confirmed an increase in dead coral and algal cover, yet maintenance of coral structure through the time periods compared in our study.

At face value, the results of our study are consistent with observations that the structure of coral reef fish communities has changed relatively little despite increases

Table 4. Tests for normality, equal variances, and equal means for family relative abudance between time periods. Familes with < 1% mean relative abundance across sites were grouped as "Other." + indicates violation of normality or equal variances assumption, ^ indicates Wilcoxin rank sum W statistic calculated, and * indicates significant differences between time periods (P < 0.05).

	Mean relative abundance (SD)		Shapiro-Wilks test W		Shapiro-Wilks test P		F test		t-test (Wilcoxon rank sum test^)	
Family	Historical	2006	Historical	2006	Historical	2006	F	P	t (W^)	P
Shallow										
Acanthuridae	1.68 (1.53)	2.76 (0.95)	0.93	0.94	0.57	0.65	2.62	0.46	−1.22	0.26
Apogonidae	16.08 (14.15)	13.77 (11.61)	0.85	0.92	0.21	0.53	1.48	0.78	0.26	0.80
Chaenopsidae	3.31 (3.19)	1.48 (0.58)	0.93	0.95	0.57	0.73	30.05	0.02+	1.26	0.27
Gobiidae	2.69 (1.16)	2.79 (1.23)	0.87	0.97	0.26	0.82	0.89	0.88	−0.13	0.90
Grammatidae	2.08 (1.37)	1.23 (1.92)	0.80	0.77	0.08	0.06	0.51	0.52	0.78	0.46
Holocentridae	6.22 (2.93)	17.54 (3.85)	0.94	0.84	0.70	0.18	0.58	0.60	−5.03	< 0.01*
Labridae	7.46 (2.26)	10.33 (4.50)	0.87	0.87	0.25	0.29	0.25	0.22	−1.26	0.25
Labrisomidae	14.34 (6.72)	14.28 (4.84)	0.97	0.92	0.88	0.52	1.93	0.62	0.02	0.99
Moringuidae	1.66 (1.71)	1.24 (0.74)	0.89	0.95	0.38	0.72	5.36	0.20	0.46	0.66
Muraenidae	3.96 (1.92)	3.91 (1.10)	0.97	0.98	0.88	0.90	3.05	0.39	0.05	0.96
Pomacentridae	8.36 (4.13)	10.63 (8.48)	0.93	0.81	0.59	0.13	0.24	0.20	−0.53	0.61
Scaridae	3.05 (2.84)	4.87 (2.74)	0.85	0.96	0.19	0.76	1.07	0.99	−0.97	0.37
Serranidae	3.88 (2.04)	1.62 (1.29)	0.93	0.85	0.57	0.22	2.50	0.48	1.92	0.10
Synodontidae	2.41 (3.03)	0.47 (0.34)	0.72	0.92	0.01+	0.55	N/A	N/A	17.00^	0.11
Tetraodontidae	1.91 (1.57)	0.93 (0.30)	0.90	0.96	0.43	0.77	28.31	0.02+	1.37	0.24
Tripterygiidae	6.84 (5.73)	4.05 (1.99)	0.88	0.97	0.30	0.86	8.27	0.11	0.92	0.39
Other	14.05 (6.65)	8.12 (3.29)	0.84	0.95	0.15	0.73	4.10	0.28	1.62	0.15

in coral mortality and algal cover, overall declines in fish abundance, overfishing of large predators, pollution, and loss of nursery habitat (McClanahan et al. 2002, Sheppard et al. 2002, Wilson et al. 2009). This interpretation, however, is an oversimplification of what is possibly an initial stage in the response of the reef fish assemblage to recent habitat disturbance. A lack of change in species diversity when reef structure is maintained has been explained by observations that even dead coral continues to provide protection and food resources to small reef fishes (Beukers and Jones 1998, Steele 1999, Almany 2004); however, Bellwood et al. (2006) demonstrated that significant shifts in community composition can occur after coral bleaching even with no apparent change in diversity metrics. Our results indicating increased representation of herbivorous fishes and observations of increased algal cover have also been documented in other areas, where herbivore proliferation has been explained by an increase in food resources resulting from algal growth on dead coral (Sheppard et al. 2002, Cheal et al. 2008, Wilson et al. 2009). Although our ANOSIM results were not significant, a trend of decreased relative abundance of planktivores [the vast majority of which were the small-bodied cardinalfishes (Apogonidae)] between the historical and 2006 sampling events was apparent. Additional data are needed to test whether the coral habitat is no longer functioning well as a shelter from predators (Munday and Jones 1998, Graham et al. 2007).

In contrast to the decreases seen in cardinalfishes, we found an increase in the relative abundance of squirrelfishes, parrotfishes, and, qualitatively, wrasses. One possible reason for the increase of such groups is a decrease in predator adundance resulting from overfishing or other impacts from human population growth (Stallings 2009). Unfortunately, the present study did not allow us to directly examine changes in predators, such as groupers and barracuda; however, a large amount of evidence of decreased densities of predators in the Caribbean (e.g., Pandolfi et al. 2003, Stallings 2010) is consistent with the hypothesis that a trend toward an increase in the relative abundance of larger-bodied fishes may be related to this decreased predation pressure.

Although algae has been shown to cause coral mortality under certain conditions (e.g., Nugues and Bak 2006, Rasher and Hay 2010), evidence suggests that shifts from coral to algae-dominant communities are initiated by the death or impairment of coral from other sources (e.g., temperature increase, disease, storm, pollution; Hughes 1994, McClanahan and Muthiga 1998, McCook et al. 2001, Aronson and Precht 2006). Regardless of the cause of mortality, it is well documented that dead coral will retain its structure for only a limited time, after which it will be eroded (Glynn 1997, Garpe et al. 2006, Pratchett et al. 2009). The time frame of structural collapse depends on numerous factors, including the coral species and duration of disturbance. Branching corals, such as *Acropora* spp., are more susceptible to erosion than non-branching taxa, losing their structural integrity on the order of 5–10 yrs (Graham et al. 2006, Pratchett et al. 2008, 2009). The sites examined around New Providence Island were dominated by non-branching species during both historical and 2006 collections, making it difficult to precisely determine the timing and cause(s) of disturbance. Our observation of the increase in herbivore relative abundance, a signature in multiple cases of a response to a relatively recent (< 10 yrs) loss of coral (Lindahl et al. 2001, Sheppard et al. 2002, Graham et al. 2006, Graham et al. 2007, Wilson et al. 2009), provides a clue regarding the potential time frame during which corals died, algae colonized, and reef fishes responded. There are mul-

tiple potential causes of coral degradation at our study sites, including the El Niño event of 1997–1998, damage from storms during the 2004–2005 hurricane seasons, ongoing pollution and/or nutrient enrichment from human developments on New Providence Island, and water temperature increases from climate change. Even with uncertainty about the exact nature of coral-algae interaction, there is general consensus that algal growth slows or limits coral recovery (McCook et al. 2001, Aronson and Precht 2006). Furthermore, recovery can be hindered by continual disturbance from storms, disease, pollution, and/or runoff (Connell 1997, Nyström et al. 2000, Aronson and Precht 2001, Chazottes et al. 2002, Carreiro-Silva et al. 2005, Fabricius 2005). Continual monitoring of these reefs and their associated fish communities will provide greater insight into the long-term effects of coral degradation on reef fish biodiversity and community structure, and allow a test of the hypothesis that the fish assemblages at these sites are responding to relatively recent disturbance.

Our ANOSIM results suggest that both shallow and deep sites have changed through time. Although a lack of replication in our study does not permit a conclusive determination, Jaap et al. (2008) noted that in contrast to the more isolated Green Cay sites that displayed typical benthic and epibenthic reef flora and fauna, the Delaporte Point sites closer to the Bahamian capital of Nassau lacked attached organisms. In addition, Stallings (2009) found negative correlations between predator abundance and human density in the Caribbean. Future surveys at additional shallow and deep sites, in regions in proximity to and isolated from urbanized areas, in conjunction with studies of anthropogenic effects, such as nutrient runoff, pollution, and sedimentation, will allow further tests of the hypothesis that proximity to human habitation is correlated with greater changes in coral habitat and associated communities.

Species Found Only at One Time Period

Most of the species collected either only historically or only in 2006 were collected from a single site in a single sample, suggesting that these species are rare and/or transient at these reefs. More than two-thirds of the historically unique reef species were collected from the deep Green Cay site (GC3). GC3 was sampled eight times historically, and it was therefore expected that rarer species would appear most frequently at this site. Similarly, more than ⅔ of the reef species collected only in 2006 included sites that were not sampled historically, thus it is not surprising that these collections included some unique species. One particularly standout singleton from the 2006 collections is the Indo-Pacific native lionfish, *P. volitans*. This introduced species has been documented in The Bahamas since 2005 (Whitfield et al. 2007, Morris et al. 2009). Recently, there has been both observational (Green and Côté 2009) and experimental (Albins and Hixon 2008) evidence that *P. volitans* is becoming more abundant and is a voracious predator on native fishes. With data now available from the historical Böhlke and Chaplin and our 2006 collections from four sites around New Providence Island prior to the lionfish population explosion, it will be important to revisit these sites to determine the effects that lionfish have on the reef fish community.

Fish Community Structure by Depth

A further result of our community assemblage comparisons was the distinct separation of sites by depth. Differences in community assemblages along depth gradients are well documented (e.g., Choat and Bellwood 1985, Greenfield and Johnson

1990a,b, McGehee 1994, Meekan et al. 1995, Friedlander and Parrish 1998, Arreola-Robles and Elorduy-Garay 2002, Donaldson 2002, Srinivasan 2003). In particular, Arreola-Robles and Elorduy-Garay (2002) found significant community differences among reef fishes in the Gulf of California at depths comparable to our shallow and mid/deep sample sites. The clustering of sites from our study conformed to documented patterns of community changes across depth, providing confidence that our historical and current samples accurately reflect the community composition.

The depth associations we found for multiple species are supported by knowledge of cardinalfishes, blennies, and squirrelfishes. Our finding of a generally shallow distribution for the cardinalfish, *Phaeoptyx conklini,* and deeper ranges for *Apogon lachneri*, *Apogon robinsi*, *Apogon pseudomaculatus*, *Apogon townsendi*, and *Phaeoptyx pigmentaria* were also reported by Greenfield and Johnson (1990a). Similarly, our results that blennies, *O. macclurei*, *Labrisomus gobio, L. guppyi*, and *Labrisomus nigricinctus,* were found primarily in shallow waters, while *L. haitiensis* generally had a deeper distribution matches the results of Greenfield and Johnson (1990b). Also, our finding that the squirrelfish, *N. marianus,* was more abundant at deeper sites is consistent with Lieske and Myers (1996). Explanations for such partitioning include larval settlement preference, differential survival in different habitats, and/or food/shelter availability (Greenfield and Johnson 1990a,b). Note that our study focused solely on depth and did not examine microhabitat preferences across a range of habitats (Srinivasan 2003).

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