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Long-Term Persistence of Coral Assemblages on the Flower Garden Banks, Northwestern Gulf of Mexico: Implications for Science and Management

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The coral reefs of the Flower Garden Banks (FGB) are among the most sensitive biological communities in U.S. Federal waters of the Gulf of Mexico. In 1973, the Minerals Management Service (MMS) established a program of protective activities at those reefs. The MMS and the National Oceanic and Atmospheric Administration (NOAA) have been monitoring coral populations on a long-term basis to detect incipient changes caused by oil and gas activities. The results also help in explaining the widespread degradation of reef ecosystems observed in the Caribbean region over the past few decades. Two sites, each 100 × 100 m and 17–26 m deep, have been monitored since 1988: one on the East FGB and the other on the West FGB. The mean coverage of living hard corals exceeded 50% at the two banks in 2002–2003, consistent with estimates of coral cover in previous years. We compared our results from 2002–2003 with data collected during the same period on protected reefs within the Florida Keys National Marine Sanctuary (FKNMS). Low values of coral cover on the reefs in the FKNMS exemplify how catastrophic mortality of the formerly dominant *Acropora* spp. led to degradation of coral assemblages throughout the Caribbean. The FGB remained in exceptionally good condition, largely for reasons of geography; their northern location excluded the cold-sensitive acroporids, so the regional-scale loss of acroporids did not reduce coral cover. The continuing multidecadal baseline of reef condition generated by the monitoring program at the FGB will enable managers to make informed decisions in the event of future changes to their biota.

The Flower Garden Banks (FGB) are part of a series of Jurassic-age salt diapirs located along the outer continental shelf of the Gulf of Mexico (Rezak et al., 1985, 1990). The caps of some of these salt domes extend upward into the photic zone, providing conditions favorable for colonization by corals, coralline algae, invertebrates, and fish. Oceanographic conditions are favorable to luxuriant coral growth at the FGB in particular, in that they are bathed primarily by warm, oceanic currents and coastal influences are relatively weak (Rezak et al., 1990; Lugo-Fernández, 1998).

The northwestern Gulf of Mexico is one of the most active offshore oil and gas exploration and production areas in the world, with a number of platforms located in close proximity to the FGB. The Bureau of Land Management (BLM)–Minerals Management Service (MMS) of the U.S. Department of the Interior began a program of protective activities at the FGB in 1974. Oil and gas exploration and production are prohibited in a "no-activity zone" immediately surrounding the banks to ~100 m depth. In addition, drill cuttings must be shunted to deep water within a 4-mile (6.7-km) "shunting zone" surrounding the banks. (See Gittings et al. [1994] for detailed discussion and maps.)

The MMS mandates required monitoring of the coral reefs of the FGB to detect any changes that may be caused by oil and gas exploration and production. That stipulated monitoring requirement ended in 1988, but MMS has continued its monitoring activities to the present. In 1992, the Flower Garden Banks National Marine Sanctuary (FGBNMS) was established under the stewardship of the National Oceanic and Atmospheric Administration (NOAA). The Sanctuary designation further reduced direct effects to the reefs by eliminating discharges of pollutants and most types of fishing (Lang et al., 2001). Anchoring was prohibited beginning in 2001. Recreational and commercial hook-and-line fishing are now the only fishing activities permitted in the FGBNMS.

The long-term monitoring effort began in 1988 (Gittings et al., 1992). This program has been continuously funded since 1988 by MMS and since 1993 by MMS in partnership with the FGBNMS. The long-term data provide the scientific basis for management of the FGBNMS. Because reefs of the western Atlantic and Ca-

ribbean have been declining over the past quarter century for a variety of reasons unrelated to oil and gas activities (Aronson and Precht, 2001; Gardner et al., 2003) and because reefs worldwide are now in decline (e.g., Wilkinson, 2000, 2002, 2004), the monitoring program has taken on the added dimension of potentially detecting regional and global change.

In this paper, we report on the condition of coral assemblages at the FGB in 2002–2003. We compare our results to previous years' data from the FGB and to data from fully protected reefs in the Florida Keys National Marine Sanctuary (FKNMS). Finally, we discuss the implications of persistently high coral cover at the FGB for understanding the regional decline of coral assemblages in the wider Caribbean.

Study Areas

The East Flower Garden Bank (EFGB) is located 193 km southeast of Galveston, TX, and the West Flower Garden Bank (WFGB) is 19 km west of the EFGB or 172 km southeast of Galveston. The coral-dominated caps of the FGB extend from 15 to 52 m water depth. In 1988–1989, a 100- × 100-m study site was established on the top surface of each bank to monitor benthic community structure (Gittings et al., 1992). The two sites contained biotic assemblages that were considered representative of their respective banks. At the EFGB, the 10,000-m^2 sampling area is centered at 27°54.52′N 93°35.84′W, is situated in a depth range of 17.4–26.2 m, and occupies 0.5% of the surface area of the reef cap. At the WFGB, the monitoring site is centered at 27°52.50′N 93°48.92′W, is located in a depth range of 18.5–25.1 m, and covers 2.0% of the surface area of the reef cap.

Materials and Methods

Transects.—The two study sites were surveyed during research cruises in Oct. 2002 and Aug. 2003. At the time of each survey, divers temporarily extended polypropylene lines around the perimeter of each study site. Crosslines were also installed, dividing the area into four quadrants. The perimeter and crosslines facilitated underwater navigation.

To estimate the areal coverage of benthic components such as corals and macroalgae, fourteen 10-m long fiberglass surveyor's tapes were positioned at each study site. Coverage was estimated from these transects using digital videography (see below). Because of the constraints on divers' bottom time, transects were placed haphazardly rather than randomly (Aronson et al., 1994; Aronson and Swanson, 1997). It was essential for divers to be able to move easily between transects, finishing one and then quickly locating the next one. In addition, previous investigators avoided large areas of sand within the study sites because the sand microhabitat was of less interest than hard substratum. The present study adopted this constraint as well, to assure comparability with the earlier data.

The transects in this study were laid in a trapline pattern. The first transect was positioned at random within one quadrant of the study site and laid in a randomly chosen compass heading. The beginning of the next transect was positioned approximately 10 m from the end of the first and laid haphazardly at an obtuse angle to the direction of the first. The third transect was laid in the same manner relative to the second, and so on. If a transect reached the border of the study site, it was reflected off the border and continued as a bent line. Each transect was marked at both ends with subsurface buoys, so that it could be located easily by divers.

The patterns generated by placement of the transects covered all four quadrants of the study areas and sampled them with approximately equal intensity. Considering the possibility of nonrandom distribution of the organisms sampled in the transects (e.g., Endean et al., 1997; Lewis, 2004) and the constraints on field time, stratifying by quadrant was deemed more desirable than the sparse sampling of areas that sometimes occurs when transects are positioned at random.

Videography.—Videography provides a logistically simpler and more reliable alternative to still photography (Aronson et al., 1994), which was used in previous surveys at the FGB. A diver swam along each transect, videotaping in plan view with a Sony DCR-VX 2000 digital video camera in an Ikelite underwater housing. The camera was fitted with a wide-angle lens and was operated in progressive-scan mode at 30 frames/sec. Illumination was provided by an Ikelite ProVideo Lite II waterproof video light with a 100-watt bulb. A depth gauge and scaling bar were attached to an aluminum bar that projected forward from the video housing. The depth gauge-scale bar assembly, which appeared in the videotaped field, provided data for each frame and also ensured that the camera remained at a constant height of 40 cm above the bottom. By holding the video cam-

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era perpendicular to the substratum and swimming slowly along the transect, it was possible to produce clear stop-action images for analysis (Aronson et al., 1994; Murdoch and Aronson, 1999).

The zoom on the camera was set so that the video frames covered a 40-cm-wide swath along each of the 10-m transects, for a total area of 4 m^2 videotaped per transect or 56 m^2 videotaped per study site per year. Each video frame was 40 × 27 cm or 1,080 cm^2. These dimensions were smaller than those of the still photographs taken in previous studies, which were 44 × 63 cm or 2,772 cm^2. The reason for the difference is that the videographic technique is designed to enable investigators to identify corals and many other sessile invertebrates to species down to a colony size of approximately 3 cm. This level of precision is not possible using video frames that record larger areas of the substratum.

Data from the digital videotapes were collected and analyzed using automated methods developed by one of us (TJTM). A set of 42 frames was captured from each video transect, using a Macintosh PowerBook G4 with the software Adobe Photoshop version 6.02 and Radius PhotoDV image-capture plug-in software. The time taken to film each 10-m transect, which averaged 150 sec, was measured and divided into 42 equal intervals. The software captured the frame at the beginning of each of the 42 intervals and applied a series of digital filters to enhance image quality. Substratum cover was estimated from 20 even-numbered frames, depicting nonoverlapping areas of substratum, from the set of 42 images. The 21st even-numbered frame was reserved as a spare in the event that a frame from among the first 20 could not be used. The odd-numbered frames, which overlapped the even-numbered frames, allowed the investigators to obtain alternative views of the areas around objects when those objects were obstructed or unclear in the even-numbered frames.

The total area analyzed from the videotapes was 30.24 m^2 per site per year (14 transects × 20 frames/transect × 1,080 cm^2/frame). In contrast, the photographic technique used in previous years covered more than twice the area, at 65.97 m^2 per site per year (14 transects × 17 frames/transect × 2,772 cm^2/frame). Despite this difference in the area covered, as well as the difference in analytical technique (point counts for the video transects vs planimetry for the photographs), a comparison of the videographic and photographic methods in 2002–2003 showed that the two approaches gave nearly identical estimates of coral cover (R. B. Aronson and W. F. Precht, unpubl. data).

After frame capture and enhancement, each even-numbered frame had a randomly selected image of 25 randomly positioned dots added as a separate layer. The substratum components under these dots were identified visually. Hard corals (Orders Scleractinia and Milleporina) were identified to species and other benthic components were assigned to functional categories: sponges, macroalgae, a combined category called CTB (crustose Coralline algae, fine algal Turfs and Bare hard substratum), and sand and other nonliving categories of substratum. The count data were entered into Microsoft Excel spreadsheets. Dots falling on the depth gauge-scale bar assembly were moved to the nearest position off the equipment and analyzed.

Quality assurance-quality control (QA-QC) consisted of three trained individuals (RBA, WFP, and TJTM) diving together on the study sites and identifying corals and other taxa. Captured video frames were then examined by all three individuals. These procedures were designed to ensure that (1) all three investigators agreed on species identifications, which was particularly a concern with respect to the *Montastraea annularis* species complex, and (2) the taxa were recognizable in the video frames. Previous QA-QC exercises, run by two of us (TJTM and RBA) with video transects from the Florida Keys, demonstrated that the data derived from video transects are of high quality. The error associated with identification of hard corals to species was <1%, with the exception of *M. faveolata* and *M. franksi,* which were difficult to distinguish in the video frames. Accordingly, we combined *M. annularis, M. faveolata,* and *M. franksi* in our diversity calculations and multivariate analysis. The error rate was also <1% in the assignment of major benthic components to their correct categories.

We noted above that our program of transect sampling was limited to the study site on each bank. Strictly speaking, the conclusions from any spatial and temporal comparisons are necessarily limited to those small areas. Generalizations about the reefs of the FGB are valid only insofar as the study sites are representative of the areas beyond; therefore, we interpret the results of univariate and multivariate analysis cautiously with respect to the FGB in general.

RESULTS

Univariate analysis.—The point counts from the video transects, grouped into major functional

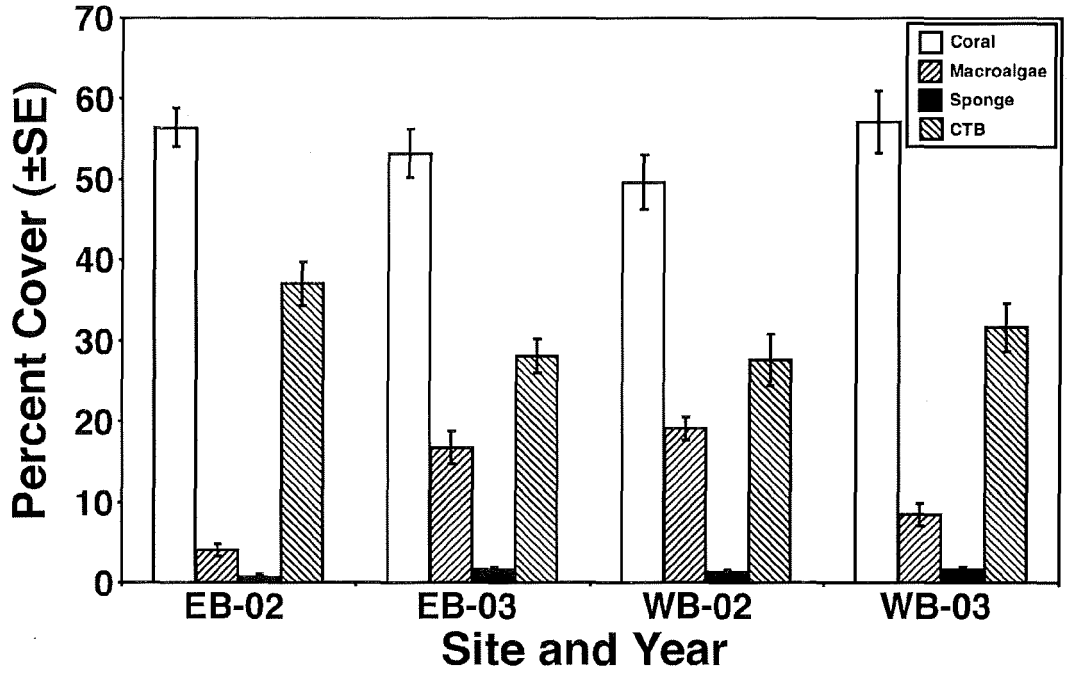

Fig. 1. Percent cover of four functional categories of sessile benthos at the Flower Gardens in 2002 and 2003. Error bars represent standard errors. Abbreviations: EB, East Bank; WB, West Bank. CTB denotes a category that combines crustose coralline algae, fine algal turfs, and bare hard substratum.

categories, were graphed as percent covers, with each transect providing an estimate of coral cover, macroalgal cover, etc. (i.e., n = 14 for each site in each year; see Aronson et al., 1994 for discussion of sample sizes). Examination of Figure 1 suggests that there were no systematic differences in the percent covers of these categories, either between the EFGB and the WFGB or from 2002 to 2003. The univariate data were then expressed as proportions and analyzed by two-way analysis of variance (ANOVA), with site and year as fixed factors. Before ANOVA, the data were tested for conformity to the parametric assumptions of normality and homogeneity of variances, using the Lilliefors and F_{max} tests, respectively. The data were transformed as necessary.

The data on the proportional cover of all living hard corals conformed to the assumptions of parametric statistics, so transformation was not necessary. A two-way ANOVA showed no significant effect of either site or year, nor was the site × year interaction significant (Table 1A). An ANOVA using arcsine-transformed, proportional cover data yielded virtually identical results.

The data on the proportional cover of sponges satisfied the assumption of homogeneity of variances, and all but one set of 14 transects were normally distributed. Arcsine transformation of the data corrected the normality problem. A two-way ANOVA showed no significant effect of site and no significant site × year interaction (Table 1B). There was an increase in sponge cover from 2002 to 2003 that was nonsignificant at $P = 0.06$. With five ANOVAs in Table 1, adjustment of α to maintain an experimentwise error rate of 0.05 renders this result decidedly nonsignificant rather than marginally so. Given the extremely low values measured for sponge cover (Fig. 1), the increase is ecologically insignificant in any case.

The data on the proportional cover of macroalgae were normally distributed, but the variances were not homogeneous. Arcsine transformation homogenized the variances. A two-way ANOVA revealed a highly significant site × year interaction (Table 1C). That interaction is clearly visible in Figure 1: macroalgal cover increased at the EFGB from 2002 to 2003 and decreased at the WFGB during the same period. The significant interaction makes it difficult to interpret the significant effect of site in Table 1C.

The fourth univariate cover category analyzed was CTB. The components of CTB are difficult to distinguish visually in the field, and

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TABLE 1. Results of two-way ANOVAs on proportional cover estimates and H' (with the *Montastraea annularis* species complex considered as a single taxon) for hard corals from the random video transects.

Source	Sum of squares	df	Mean square	F ratio	*P* value
A. Hard corals (untransformed)					
Site	0.0028	1	0.0028	0.1982	0.658
Year	0.0063	1	0.0063	0.4429	0.509
Site × year	0.0400	1	0.0400	2.8281	0.099
Error	0.7348	52	0.0141		
B. Sponges (arcsine transformed)					
Site	0.0040	1	0.0040	1.1761	0.283
Year	0.0128	1	0.0128	3.7050	0.060
Site × year	0.0033	1	0.0033	0.9655	0.330
Error	0.0179	52	0.0034		
C. Macroalgae (acrsine transformed)					
Site	0.0543	1	0.0543	6.6303	0.013
Year	0.0089	1	0.0089	1.0913	0.301
Site × year	0.5474	1	0.5474	668.01	<0.0005
Error	0.4261	52	0.0082		
D. CTB (untransformed)					
Site	0.0124	1	0.0124	1.1577	0.287
Year	0.0086	1	0.0086	0.8009	0.375
Site × year	0.0586	1	0.0586	5.4914	0.023
Error	0.5552	52	0.0107		
E. Shannon–Wiener diversity, H' (untransformed)					
Site	0.1272	1	0.1272	0.8881	0.350
Year	0.0528	1	0.0528	0.3687	0.546
Site × year	0.0102	1	0.0102	0.0710	0.791
Error	7.4453	52	0.1432		

they are even more problematic in still photographs and video transects. All three connote high levels of physical disturbance or herbivory (or both); therefore, it is reasonable to combine them (Aronson and Precht, 2000). The CTB data conformed to the assumptions of normality and homogeneity of variances and were not transformed. A two-way ANOVA revealed a site × year interaction that was marginally significant at $P = 0.023$ after adjustment of α (Table 1D). This interaction was in the opposite direction from that in macroalgal cover: for CTB, cover declined at the EFGB and increased at the WFGB from 2002 to 2003.

The Shannon–Weiner diversity index, H' was calculated for hard corals from the proportional, species-specific data as follows:

$$H' = -\sum_{i=1}^{k} p_i \ln p_i, \qquad (1)$$

where k is the number of species present, p_i is the proportional cover of the ith species, and ln is the natural logarithm. Mean H' ranged from a low of 1.09 at the WFGB in 2002 to a high of 1.25 at the EFGB in 2003 (mean H' was 1.13 at the WFGB in 2003 and 1.16 at the EFGB in 2002). The data conformed to the assumptions of normality and homogeneity of variances. A two-way ANOVA showed no significant effect of either site or year, and the site × year interaction was not significant (Table 1E).

Minimum detectable difference.—The goal of the video transecting methodology is to be able to detect the smallest biologically meaningful changes in percent coral cover with high power at $\alpha = 0.05$. We consider a change of 5–10% coral cover to be biologically meaningful, which is a stricter criterion than the 10–20% figure obtained by M. J. Risk and A. C. Risk (1997) in a poll of reef scientists.

The minimum detectable difference, δ, was calculated for the two-way ANOVA on proportional coral cover from the video transects following Zar (1984). The significance level was set at the conventional $\alpha = 0.05$ and the desired power at the conventional $(1 - \beta) = 0.80$. For videographic surveys of two sites over 2 yr, with 14 transects per site per year, δ =

TABLE 2. Species of hard corals observed in the two study sites in 2002–2003. All species were detected at both sites except *Madracis mirabilis*, which was only seen at the EFGB. *Porites porites* has not appeared in previous species lists; its occurrence at the FGB is uncertain, given the difficulty of distinguishing it from *P. furcata* in some situations.

Class: Order	Family	Species
Hydrozoa: Milleporina	Milleporidae	*Millepora alcicornis*
Anthozoa: Scleractinia	Astrocoeniidae	*Stephanocoenia intersepta*
	Agariciidae	*Agaricia agaricites*
		Agaricia fragilis
		Leptoseris cucullata
	Pocilloporidae	*Madracis decactis*
		Madracis mirabilis
	Siderastreidae	*Siderastrea siderea*
	Poritidae	*Porites astreoides*
		Porites furcata
		Porites porites
	Faviidae	*Colpophyllia natans*
		Diploria strigosa
		Montastraea annularis
		Montastraea cavernosa
		Montastraea faveolata
		Montastraea franksi
	Mussidae	*Mussa angulosa*
		Scolymia cubensis

0.074. We can expect to be able to detect a 7.4% change in coral cover between any 2 yr at the FGB, or a 7.4% difference in cover between the two banks in a 2-yr study. In other words, if ecologically important changes in coral cover occur in the future, the sampling approach used in this study can be used to detect them.

The calculated δ agrees with values of 5.2–9.8% obtained using the video method to compare four sites in Florida and the Caribbean, with 10 transects per site and coral cover varying from 3% to 21% (Aronson et al., 1994). The δ calculated in this study is a few percent higher than the minimum detectable difference of 2.4–3.8% calculated by Murdoch and Aronson (1999) for a comparison of three sites in the Florida Keys; however, that study used 30 transects per site and the sites had extremely low cover, both of which reduced the error variance and thus reduced δ.

Multivariate analysis.—A total of 19 species of hard corals belonging to 12 genera were recorded in visual surveys of the two study sites in 2002–2003 (Table 2). As in previous surveys at the FGB, the *M. annularis* species complex dominated the coral assemblage. The five most abundant coral taxa in terms of areal coverage were the *M. annularis* complex (grand mean of percent cover 31.90%; the mean of the 56 transects from both sites in both years), *Diploria strigosa* (grand mean 6.35%), *Porites astreoides* (grand mean 4.92%), *M. cavernosa* (grand mean 3.39%), and *Colpophyllia natans* (grand mean 1.81%).

The point counts of hard corals in the videotaped transects were analyzed by species, using multivariate statistical techniques. Multivariate coral cover was compared between sites and years using analysis of similarity (ANOSIM) on untransformed data, with the three species of the *M. annularis* complex combined. There were no significant differences between sites (Global R = 0.01, $P = 0.26$) or years (Global R = −0.09, $P = 0.60$). A single-factor ANOSIM on the four sets of 14 transects also showed no significant differences (Global R = 0.001, $P = 0.41$), meaning that there was no multivariate interaction; this conclusion was confirmed by pairwise ANOSIM tests on the four sets of transects (see Clarke and Gorley, 2001).

To place the data on coral cover in a regional context, we ordinated the multivariate coral cover data using nonmetric multidimensional scaling (MDS). We pooled the species-specific point-count data for hard corals from the 14 transects from each survey at a site in 1 yr. Square root-transformed Bray-Curtis dissimilarity matrices were calculated from the vectors

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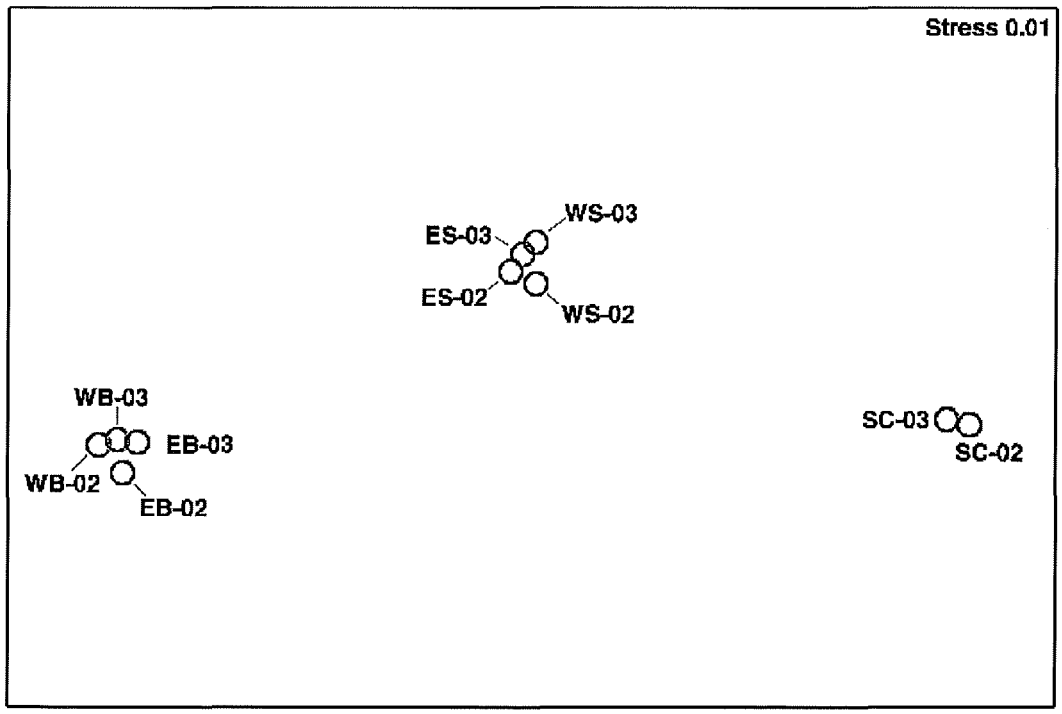

Fig. 2. Two-dimensional, nonmetric MDS plot based on square root–transformed Bray–Curtis dissimilarities, comparing multivariate coral cover from video transects between the FGBNMS and three FPZs in the FKNMS. The three species in the *M. annularis* complex were pooled for this analysis. The video transects were shot in 2002 and 2003. The FGBNMS sites form a discrete, tight cluster of points distinct from the Florida sites, reflecting high coral cover and low variability in species composition. FGBNMS abbreviations: EB, East Flower Garden Bank; WB, West Flower Garden Bank. FKNMS abbreviations: SC, South Carysfort Reef FPZ; WS, Western Sambo Reef FPZ; ES, Eastern Sambo Reef FPZ.

representing species-specific point-count values from the pooled transect data.

We included in the analysis, pooled point-count data from random transects videotaped in three fully protected zones (FPZs) of the FKNMS during the same period. Ten 25-m transects were videotaped at each site each year at 13.5–17.4 m depth. Fifty nonoverlapping frames were analyzed per transect with 10 point counts per frame, for a total of 500 points per transect as in this study (unpubl. data, R. B. Aronson and T. J. T. Murdoch). The mean cover of hard corals ranged from 1.00% to 7.10% in the six data sets of transects from Florida. Note that although the transects at the FGB were slightly deeper, water clarity is generally higher than it is along the Florida reef tract; this means that we sampled equivalent biological zones in both locations.

The MDS placed the FGB in a tight group, well-separated from the three FPZs in the Florida Keys, for which one site, South Carysfort Reef, clearly separated from the other two (Fig. 2; South Carysfort is also separated geographically from the other two FPZs). The stress level of the MDS was a low 0.01, indicating high confidence in the pattern displayed. Not only is coral cover higher at the FGB than along the Florida reef tract, but it also may be more uniform in species composition from reef to reef (see also Murdoch and Aronson, 1999).

Discussion

The species richness of hard corals is low at the FGB, with 23 species from 14 genera represented at 17–50 m depth (E. L. Hickerson, pers. comm.). Our species list for the study sites in 2002–2003 was essentially identical to the lists for previous years (Gittings et al., 1992; Dokken et al., 2003). Generic and specific richness were lower within the 10,000-m^2 study sites than on the banks as a whole, which was not surprising, considering their small size and limited depth range. The majority of genera and species were in fact represented in the study sites. Our values of H' and the order of coral

species dominance were consistent with previous studies, which also combined the three species in the *M. annularis* complex in their diversity calculations.

The overall species list for the two banks, which now includes *Acropora palmata* (see below), compares to 67 species from 24 genera found on some Caribbean reefs (Porter and Tougas, 2001). Scleractinian species characteristic of shallow-water habitats (i.e., shallow fore reefs, reef crests, and back reefs) were not represented in the past on the FGB, and in particular, the cold-sensitive acroporids were conspicuously absent. A single colony of *A. palmata* was discovered on the WFGB in 2001, however, and it was still present in 2004. This colonization event, along with the recent appearance of isolated colonies of *A. palmata* and large stands of *A. cervicornis* along the east coast of Florida, could represent an incipient range expansion of Atlantic acroporids related to global warming (Precht and Aronson, 2004). On the other hand, acroporid populations along the Florida reef tract have proven extremely volatile on a multidecadal scale (Jaap and Sargent, 1994; Jaap, 1998), so a definitive test of the range-expansion hypothesis will require continued long-term observations.

The reef communities of the FGB are characterized by low macroalgal cover, high abundances of predatory and herbivorous fishes, and coral cover that is extremely high compared with other reefs in the hemisphere (Pattengill-Semmens and Gittings, 2003). Coral assemblages at the two study sites remained in excellent condition at the time of this study; coral cover ranged from 40% to 60% from 1988 through 2003 (Gittings, 1998; Dokken et al., 2003; this study). The cover of sponges was low as in previous surveys. Macroalgae and CTB fluctuated in a reciprocal pattern, as they often do elsewhere (Aronson and Precht, 2000). The shallow-water gorgonian fauna is absent from the coral cap of the FGB, although gorgonians (and antipatharians) are conspicuous constituents of the reef communities below 50 m depth. The absence of a shallow-water gorgonian fauna is probably a result of oceanographic isolation from the rest of the Caribbean (Jordán-Dahlgren, 2002).

The high coral cover of reefs at the FGB contrasts markedly with the degraded state of reefs throughout the southern Gulf of Mexico, Florida, the Bahamas, and the Caribbean. Reasons for the exceptional condition of the FGB include (1) the water depth of the reefs, which buffers them from the effects of storm waves and anomalously high summer sea temperatures, (2) the remote, offshore location of these reefs, which limits human access and exposes them to oligotrophic, oceanic waters, and (3) protective Federal regulations, which help prevent hydrocarbon-related effects, as well as effects from fishing and recreational diving. In the rest of the Caribbean, however, even protected, offshore reefs, far from centers of human population, have lost much of their coral cover (McClanahan et al., 1999; Aronson and Precht, 2001). Thus, it is also important to consider regional processes. In particular, the historical absence of acroporid corals from the FGB accounts in large part for their persistently high coral cover.

Acropora palmata and *A. cervicornis* were dominant space occupants of fore-reef habitats on many reefs throughout the Caribbean region (sensu lato) for thousands of years until the 1980s. The loss of these two acroporid species, principally because of historically unprecedented outbreaks of white-band disease, reduced coral cover and opened space for colonization by fleshy and filamentous macroalgae (Aronson and Precht, 2001). Because most of the recent change has resulted from acroporids being subtracted from coral assemblages, coral cover remained high on reefs where massive corals dominated before (and after) the 1980s, including heavily fished reefs in Jamaica (Edmunds and Bruno, 1996). The FGB apparently did not have acroporids in recent times; therefore, they had none to lose, and as a result massive corals continuously monopolized the open surfaces of the reef caps. This effect clearly has far more to do with the high-latitude location of the FGB, which excluded *Acropora* spp., than it does with their protected status, considering that the study reefs in Florida are fully protected. Coral assemblages at the FGB are similar to those in Bermuda, where (1) values of coral cover can also reach or exceed 50%, (2) massive corals of the genera *Montastraea, Diploria,* and *Porites* dominate, and (3) *Acropora* spp. are absent because the water historically has been too cold during the winter (Dodge et al., 1982; Bright et al., 1984; Logan, 1988; Webster and Smith, 2002).

Massive corals have also declined on some Caribbean reefs (Lang, 2003), a secondary effect that has accentuated the difference in coral cover between those reefs and the FGB. Diseases were observed on massive corals at the FGB in 2002–2003, but their prevalence was low compared with most other reefs that have been surveyed around the Caribbean. The short- and long-term effects of disease on coral populations remain difficult to assess at these

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sites, although disease is clearly a factor in the mortality of some corals at the FGB. Specifically, plague-like syndromes were observed on a number of species, including the *M. annularis* species complex, *M. cavernosa, C. natans,* and *D. strigosa.* Environmental stressors such as pollution, nutrient loading, and elevated temperature may be associated with outbreaks of marine diseases, yet few firm causal connections have been established (Harvell et al., 2004). Nevertheless, accumulating evidence supports the hypothesis that outbreaks of coral disease have increased recently in the Caribbean (Aronson et al., 2002; Ward and Lafferty, 2004).

Coral bleaching in response to anomalously high summer-season temperatures has also become more frequent since the 1980s (Hoegh-Guldberg, 1999). Minor bleaching episodes occurred sporadically at the FGB during the 1990s and were followed by recovery of most of the affected coral colonies (Hagman and Gittings, 1992; Dokken et al., 2003; Pattengill-Semmens and Gittings, 2003). As in the rest of the Caribbean, other causes of lethal and sublethal coral mortality on the FGB include the establishment of territories by damselfish (Pomacentridae), predation by parrotfish (Labridae: Scarinae) and other mobile fauna, aggressive interactions between coral colonies and between corals and other benthic organisms, and the toppling of colonies as a result of bioerosion. The persistence of coral cover at the 50–60% level at the FGB strongly suggests that coral growth and recruitment are essentially in balance with coral mortality.

Previous monitoring efforts have provided the critical database for management decisions at the FGB. Judging from the recent arrival of a single colony of *A. palmata,* the loss of the sea urchin *Diadema antillarum* during the regional mass mortality of 1983–1984, and the recent occurrence of hurricanes and bleaching events (Gittings et al., 1994; Lugo-Fernández, 1998; Precht and Aronson, 2004), these coral reef ecosystems could change in the long term. The causes of future change can be identified and differentiated, assuming that the good condition of the current study sites is representative of the two reef caps in general. Our qualitative observations in 2002–2003 and the earlier observations of previous investigators suggest that the study sites are indeed representative.

We must continue to follow the ecological dynamics of the FGB on a multidecadal scale appropriate to the turnover times of the corals, and we must recognize that some hypotheses cannot be tested in our lifetimes. Understanding future degradation, or future improvement for that matter, is a far more daunting task on reefs such as those in the Florida Keys, which are already badly degraded. The reefs of the FGBNMS will serve as excellent models for understanding the general causes of stability and change in reef systems through time and space.

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