

**SPATIAL AND TEMPORAL VARIABILITY DURING PERIODS
OF "RECOVERY" AFTER MASS BLEACHING ON
WESTERN ATLANTIC CORAL REEFS**

CORAL BLEACHING PROJECT

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SYNOPSIS. Western Atlantic coral reefs were differentially affected by a mass bleaching (discoloration) event in 1987. We periodically assessed the "appearance" of zooxanthellate organisms between December 1987 and June 1988 at nine conspicuously affected sites in the Bahamas, Florida, St. Croix, and Venezuela, using a standardized point-count technique. Three to four months after the local initiation of the event, the "bleached" state was still present in one to three of the most abundant reef coral taxa and in a few of the less common species ($n = 5$ sites). "Recovery" occurred somewhat faster at shallower depths, at least in the Bahamas and Florida. Scleractinian corals which were "prolonged bleachers" had foliaceous or massive, rather than branching, morphologies. "Bleached" points disappeared from the point counts after +6 to +8 months.

Long-term field data on spatial and temporal variability in the dynamics of zooxanthellate organisms would help us to understand the ecological consequences of bleaching. More generally, we need to distinguish anthropogenic changes in the structure and functioning of reef ecosystems from those which occur naturally. Point-count techniques are well suited for collaborative studies involving rapid quantification of coloration states and health in reef corals.

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INTRODUCTION

Many reef corals and other organisms with endosymbiotic zooxanthellae (photosynthetic dinoflagellates) respond to conditions of stress by "bleaching"—losing zooxanthellae and/or losing photosynthetic pigments from the algae remaining in their soft tissues (e.g., Kleppel *et al.*, 1989). Prolonged bleaching of reef corals is associated with reductions in soft tissue biomass, sexual reproduction, and growth. Local discoloration of reef cnidarians has been reported throughout the past century, yet "mass" bleaching events distributed over large geographic areas have been noted only within the last decade. Extraordinary levels of bleaching on many Indo-Pacific coral reefs in 1982–83 coincided with a major El Niño–Southern Oscillation event and were followed by considerable mortality of affected organisms. Bleaching was noticed in relatively few areas of the Atlantic Ocean (reviewed by Coffroth *et al.*, 1990; Glynn 1990, 1991).

During the summer and fall of 1987, however, zooxanthellate reef cnidarians throughout the southwestern and central Caribbean, Florida and the Bahamas suddenly paled (Williams and Bunkley-Williams, 1990a). A collaborative field effort was subsequently proposed to obtain comparative information on the ecological impacts of mass bleaching (Ogden and Wicklund, 1988). Notwithstanding delays in initiating this study, our data illuminate the temporal and spatial complexity of changes in the "appearance" of zooxanthellate cnidarians during periods of "recovery" ranging from three to eleven (+3 to +11) months after the bleaching event had begun at any given locality.

SURVEY METHODS

An appeal for assistance was circulated among the regional marine laboratories and scientists, particularly members of the Association of Marine Laboratories of the Caribbean. Respondents were asked to complement any on-going bleaching studies with a plotless, chain (or weighted tape) protocol as follows (Anon, 1988): Choose specific reefs on the basis of accessibility and

generality, but survey one or more habitats which locally have been most affected by the 1987 bleaching event. Haphazardly locate five transects, each 20 m long, at a depth near the middle of any site. Record the identity of each sessile organism (or, in the event of layering, only the uppermost) occurring under the chain at premarked, 10-cm intervals. Score the "appearance" of all potential bleachers at these points on a five-point scale ranging from "normal," through "pale," "bleached," "just dead" (i.e., within the previous few days) or "recently dead" (i.e., within the previous few weeks). (Our original instructions were to restrict the two "dead" states to bleaching-related mortality. In practice, we were seldom able to determine the cause[s] of death and this stipulation was ignored.) Try to judge how rapidly the "appearance" states of the corals which had bleached was changing when deciding whether to repeat the transects at monthly intervals for a period of three months or bimonthly over six months. Measure ambient seawater temperature at a depth of 3 m during each survey. Transfer the data to the summary sheets using a standardized nomenclature. (The taxonomically unresolved *Montastraea annularis* [Knowlton *et al.*, 1992] and *Agaricia agaricites* complexes were each coded as a single taxon.)

The point-count data for all the transects in a given survey were summarized, coded and entered into a data base. We have compared the distribution of numbers of points among the different "appearance" states for all live reef corals or for individual taxa. Certain combinations of non-"normal" states were made when necessary to eliminate structural zeros or low cells. Sites were not surveyed the same number of times, nor were reefs with all combinations of depth and habitat sampled at each geographic area. Hence, the data cannot be analyzed in one large, balanced design to simultaneously compare spatial, temporal and environmental variation in bleaching and recovery. Firstly, we examined subsets of the data which could be analyzed in a single balanced design, using a hierarchical log linear procedure (SPSS procedure hiloglinear [Norusis, 1985]) in which "appearance" states (as

TABLE 2. Relative distribution among the "visible appearance" states for the pooled, normally-zooxanthellate reef corals (=scleractinians, milleporans), ordered by time in months after local initiation of bleaching at each site.^a

Site ^a	Depth (in m)	Time ^c	Percent all reef corals					N
			"Normal"	"Pale"	"Bleached"	"Just dead"	"Recently dead"	
CB	8-10	+3	70.0	23.2	5.8	0.9		534
		+4.5	77.3	15.8	2.2	4.7		555
		+6	81.2	14.9		3.9		437
RG	3-5	+3.5	59.9	38.2	1.6		0.3	319
		+6	69.6	30.1			0.3	382
		+8	97.5	2.5				320
SP	11-13	+3.5	71.5	20.2	6.7	0.5	1.0	193
		+6	78.3	20.8	0.4		0.4	240
		+8	96.4	3.6				195
CG	3-4	+4	88.0	8.0	1.4		2.6	274
		+7	88.3	10.9	0.4		0.4	468
PT	5-6	+4	82.4	13.5	4.1			364
		+7	81.2	11.7	4.9	0.2	2.0	410
EC	3	+6	90.4	9.6				157
		+9	98.8				1.2	170
M	7-10	+6	62.9	27.8			9.3	388
		+9	72.8	12.4			14.8	459
EDR	4-8	+7	78.2	7.4			14.4	353
		+10	87.8	2.9			9.3	312
LK	6-9	+8	82.4	11.1			6.5	414
		+11	80.9	11.5			7.6	514

^a Blanks indicate values of zero.

^b See Table 1 for site names.

^c Time after local initiation of bleaching, in months.

presence of a significant three-way interaction (partial chi-square = 12.13, $P = 0.0164$, 4 df) indicates that bleaching and/or recovery varied at each of the sites. In other words, the proportion of reef coral points which were affected, and their subsequent change in "appearance," was variable among these five sites.

Temporal relationships

Most zooxanthellate gorgonians and zoanths had a "normal" coloration at the time of the first point-count surveys, between +3 months and +8 months after bleaching had begun at any given locality. The percentage of reef coral points which were observed as "bleached" ranged from zero in Florida (at +6 to +8 months, 4 sites) to 6.7% at South Perry (at +3.5 months); the corresponding range for "pale" was 7.4% to 38.2%. A progressive decrease in the proportion of points in the "bleached" and/or "pale" states was noted over time at each of six sites, along with a corresponding

increase in the proportion appearing "normal" (Table 2). On a site by site basis (Table 3), these temporal changes were significant at Cane Bay, Rainbow Gardens, South Perry, Elkhorn Control, and at Molasses (where some of the differences can be attributed to an increase in the number of points in the "recently dead" state, Table 2). A slight increase between +4 months and +7 months in the proportion of "pale" points at Caño Grande (Table 2) was caused by a marked elevation of this state (6/179 in March versus 35/317 in June) in *Colpophyllia natans*, the local dominant (Table 1).

During the final surveys in June 1988, the "bleached" state was in low abundance (0-4.9%) in reef corals at all sites (Table 2). Variation among sites showed no simple relationship to "initial severity" of bleaching, time available for recovery, habitat, depth or geographic location. Between 96.4% and 98.8% of the reef coral points were considered "normal" in the Bahamas and at

TABLE 3. Results of two way tests of independence between the pattern of bleaching (distribution of numbers of points among the five "appearance" states) and specified sites, times and depths.

No.	Comparison	Chi-square	df	Adjusted significance ^c
Between times, within a site:				
1	CB ^a + 3 ^b vs. + 4.5 vs. + 6	59.268	6	S
2	RG + 3.5 vs. + 6 vs. + 8	137.037	4	S
3	SP + 3.5 vs. + 6 vs. + 8	62.137	4	S
4	CG + 4 vs. + 7	9.983	2	NS
5	PT + 4 vs. + 7	3.464	2	NS
6	EC + 6 vs. + 9	11.623	1	S
7	M + 6 vs. + 9	33.91	2	S
8	EDR + 7 vs. + 10	11.832	2	NS
9	LK + 8 vs. + 11	0.451	2	NS
Between times, pooled sites:				
10	CB, RG, SP, CG, PT at +3/4 vs. +6/7	25.08	2	S
11	RG, SP, EC, M at +6 vs. +8/9	87.002	1	S
Between sites, within a geographic area: ^d				
12	EC + 6 vs. M + 6	43.104	2	S
13	EC + 9 vs. M + 9	52.399	2	S
14	RG + 3.5 vs. SP + 3.5	26.467	2	S
15	RG + 6 vs. SP + 6	5.659	1	NS
Between sites and geographic areas: ^d				
16	CB + 3 vs. SP + 3.5	1.093	2	NS
17	CB + 6 vs. SP + 6	8.559	2	NS

^a See Table 1 for site names.

^b Time after local initiation of bleaching, in months.

^c α , the significant level of the critical value, is 0.05/17, i.e., 0.003.

^d Tests were made for three-way interactions (using data in 12 and 13, 14 and 15, 16 and 17, respectively), but none were significant after applying the Bonferroni correction.

Elkhorn Control, comparable to values (>99%) from the as-yet "unbleached" Bermudian sites in May (Cook *et al.*, 1990). However, at Molasses Reef (the closest of the other Florida sites to Elkhorn Control), the corresponding figure was only 72.8%. "Normal"-appearing reef corals constituted 80.9% to 88.3% of the points in Venezuela and at the remaining two sites in Florida.

When the data at +3/4 months for St. Croix, the Bahamas and Venezuela are combined and compared to the pooled data at +6/7 months for the same five sites, the difference in the distribution among the "appearance" states is significant (Table 3-10). Similarly, the pooled data at +8/9 months for the Bahamas and the northern Florida Keys are significantly different from the corresponding data at +6 months for these four sites (Table 3-11).

Spatial relationships

Comparisons between the different sites incorporate potentially important environ-

mental effects, some of which vary with depth. Apparent "depth effects" must be explored with caution, given our lack of site replication (Hulbert, 1984). Regardless of the initial severity of the mass bleaching event at any given site, recovery seemed to occur more rapidly at shallower habitats in the Florida Keys (Hallock, personal observation; Jaap, personal observation; Muller, personal observation; B. D. Causey, personal communication) and the Bahamas (Lang *et al.*, 1988). Indeed, for both March and June, a significant difference between Molasses (7-10 m) and Elkhorn Control (3 m) was due to a higher proportion of the reef coral points being scored as "pale" and "recently dead," and a lower proportion as "normal," at the deeper of these two sites (Table 3-12, 3-13, respectively). In the mid-January 1988 counts in the Bahamas, however, the significant differences between 3-5 m (Rainbow Gardens) and 11-13 m (South Perry) were due to proportionately fewer "normal" and "bleached" points, and a

higher proportion of "pale" points, on the shallower reef (Table 3-14). Differences between the two Bahamian sites were no longer significant 2.5 months later (Table 3-15), although the proportion of "normal" points at South Perry still exceeded that at Rainbow Gardens.

Unless their initial conditions were similar, there was little resemblance among sites of comparable depths in different geographic areas. For instance, the reef coral data collected at +3 months in Cane Bay and at +3.5 months at South Perry are statistically indistinguishable, as are those at +6 months for both sites (Table 3-16, 3-17). In contrast, reef corals in northwestern Venezuela showed fewer prolonged effects of the mass bleaching event than those in the Bahamas. As expected, the three-way interaction between site (Caño Grande and Rainbow Gardens), time (+3.5/4 months and +6/7 months) and "appearance" state (as "normal" versus "affected") is significant (partial chi-square = 68.86, $P = 0.0001$, 1 df), as are all the two-way interactions.

Individual taxa

A common (though not understood) observation of bleaching events is that the specific reef corals which are most likely to discolor vary among sites (e.g., Glynn, 1990; Williams and Bunkley-Williams, 1990a; Coffroth et al., 1990). Such an effect is also evident in our data. For example, *Diploria labyrinthiformis* was considered a good indicator of prolonged bleaching at 8–10 m in Cane Bay (Gladfelter, personal observation). Bleaching and recovery of the widely distributed "*Montastraea annularis*" complex was assessed at the five sites surveyed both at +3/4 months and at +6/7 months. As in the overall data set, there is a significant three-way interaction between "appearance" state ("normal" versus "affected"), site and time (partial chi-square = 33.26, $P = <0.0001$, 4 df), indicating that the temporal changes in "appearance" (a function of bleaching and recovery) differed among the sites.

At +3/4 months, i.e., once the recovery had begun any given site ($n = 5$), prolonged discoloration was still evident in one to three of the most abundant reef corals and several

other taxa (Table 4). Between +6 months and +7 months after the event had begun at any locality, "bleached" points occurred at only 3/8 of the sites surveyed (Table 2), while the total number of discolored taxa had declined slightly (from 8 to 6). "Bleached" points were recorded in the "*Montastraea annularis* complex" at South Perry and Punta Tucacas, in the "*A. agaricites* complex," *Agaricia tenuifolia* and *Millepora alcicornis* at Punta Tucacas, and in *Colpophyllia natans* and *Stephanocoenia intersepta* at Caño Grande. No bleaching was found at the six sites surveyed between +8 and +11 months after the initiation of mass discoloration ($n = 7$ surveys). At Looe Key, the proportion of "pale" points was significantly greater at +11 months than at +8 months in the zoanthid, *Palythoa caribaeorum* (chi-square = 12.344, $P = 0.0004$, 1 df).

Five of the scleractinian corals that exhibited prolonged bleaching have predominantly massive morphologies (*Colpophyllia natans*, *Diploria labyrinthiformis*, the "*Montastraea annularis* complex," *Porites astreoides*, *Stephanocoenia intersepta*) and three are foliaceous (the "*Agaricia agaricites* complex," *A. tenuifolia*, *Leptoseris cucullata* [= *Helioseris cucullata*]). The milleporan, *M. alcicornis*, is primarily an encruster. Several of the rapidly growing, branching taxa (*Acropora cervicornis*, *A. palmata*, *Porites porites*, "finger *Porites*"), which are known to have been affected by the mass bleaching event at these sites (Hudson, 1988; Jaap, 1988; Lang et al., 1988; Losada, 1988), are presumed to have mostly recovered before the point-count surveys began. Many of the initially discolored specimens of *A. cervicornis* at South Perry, however, were dead in early November 1987 (Lang et al., 1988; Williams and Bunkley-Williams, 1990a).

OVERVIEW

In the hopes of improving community-level collaborations among reef ecologists, we first highlight the weaknesses of this regional study and suggest how some of its deficiencies might be overcome. By design, the choice of sites was skewed towards "worst cases," resulting in an underesti-

potential collaborators to respond more readily when requests arrive before the immediate effects of a perturbation have peaked.

In retrospect, the surveys were terminated too soon. Tissue biomass and reproduction in colonies of the "*M. annularis* complex" were affected by prolonged bleaching in northern Florida during summer 1988 (Szmant and Gassman, 1990). The spring recovery notwithstanding, by June 1988 we might have been witnessing the beginning of a few "reversals." (*Palythoa caribaeorum* frequently discolors in summer at Looe Key [Causey, 1988; personal communication], as does *Colpophyllia natans* at Caño Grande [Losada, personal observation].) How to evaluate the higher proportion of "recently dead" counts in Florida compared to the three other geographic areas remains unclear. Moreover, the addition of comparative, seasonal data on the coloration (see Gates, 1990) and mortality of reef corals in a non-mass bleaching year could have provided an invaluable "yardstick" against which to relate the effects of the 1987 event and subsequent perturbations (Cook *et al.*, 1990; Goreau, 1990; Williams and Bunkley-Williams, 1990b; Savina, 1991, personal communication).

There is considerable geographic variation in the "normal" *versus* "pale" coloration of western Atlantic reef corals (Jaap, personal observation; Lang, personal observation). We strongly recommend that, as in our study, "bleaching surveys" should be made by, or at least in close association with, observers having extensive *local* experience. High levels of intracolony variation are also common whenever zooxanthellate organisms bleach in nature (*e.g.*, Glynn, 1990; Williams and Bunkley-Williams, 1990a). We found that "appearance" can be described at discrete points with relative ease in the field. Our coloration data are likely to be more accurate than those obtained by visual inspection along linear intercepts or at the scale of entire colonies (Lang, personal observation). At any rate, the temporal "recoveries" evident in our data resemble those obtained elsewhere in the greater Caribbean region (Goenaga *et*

al., 1989; Porter *et al.*, 1989; Zea and Duque, 1989; Ghiold and Smith, 1990; Goreau and Macfarlane, 1990; Bunkley-Williams *et al.*, 1991).

In brief, our major errors were to start late, quit prematurely and expend proportionately too much effort on organisms lacking zooxanthellae. Nevertheless, we have demonstrated that temporal and spatial (site, depth) effects in the prolonged bleaching responses of western Atlantic reef corals are significant, perhaps explicating some of the variation detailed by Williams and Bunkley-Williams (1990a). The urgent need to implement long-term, international monitoring programs for coral reef ecosystems has been well documented, and there is currently much discussion about choice of relevant protocols (*e.g.*, Kenchington and Hudson, 1988; Miller, 1988; Ogden and Wicklund, 1988; Rogers, 1988; D'Elia *et al.*, 1991). Regionally standardized point-count techniques are appropriate for community-level assessments of color and health in reef corals, particularly when rapidity, simplicity, economy and broad applicability are important constraints.

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