Perturbation and change in coral reef communities

(*Acropora cervicornis*/spatial analysis/Dry Tortugas/temperature effects)

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ABSTRACT   Ninety-six percent of surveyed shallow-water Dry Tortugas reef corals died during the severe winter of 1976–1977. Data from skeletal stains indicate that death occurred during the mid-January intrusion of 14°C water onto the reef. In deeper water, community parameters such as percent cover, species number, and relative abundance showed no significant change. However, an analysis of competitive interactions at the growing edges of adjacent colonies reveals a 70% reduction in space competition during this environmental disturbance. These results can explain high variability in the growth rate of Floridian reefs and demonstrate the importance of obtaining long-term spatial information to interpret successional dynamics of complex communities.

Successional changes in complex natural communities are among the most difficult ecological phenomena to measure due to the often subtle influence of controlling mechanisms, the posited great length of time between observable changes, and the large sample size required to generalize with statistical confidence. In this study we report changes in coral reef community structure that occurred during the climatically severe winter of 1976–1977 (1–3).

Corals require space for plankton capture by their tentacles and adequate surface area for photosynthetic light capture by their intracellular symbiotic algae (4–6). They compete for space both intra- and interspecifically by overtopping one another and by extracoelenteric destruction, whereby the mesenterial digestive filaments of a dominant species extend onto the living tissues of an adjacent subdominant and destroy it (7, 8). Abilities in these competitive mechanisms are species-specific and, in areas of high densities on the reef, have been shown to affect coral abundance and distribution patterns (7–15). To examine competitive interactions during succession, representative subtidal quadrats containing 20 m² each of reef substrate were permanently staked and photographed with eighty 0.25-m² frames in July 1976 and rephotographed in June 1977 (Figs. 1 and 2).*

Colonies of *Acropora cervicornis*, 1 m outside of the photoquadrats, that were stained with alizerine red S (18) in July 1976 were collected in June 1977 and longitudinally sectioned. Growth since staining was determined by measuring the distance from the outer edge of the stain to the tip of the apical polyp. All colonies from a depth of 1.3 m were dead, but during the interval before their death they had grown an average (±SEM) of 25.4 ± 7.3 mm ($n = 27$); those from a depth of 13 m were still living and had grown roughly twice as much—46.7 ± 23.8 mm ($n = 5$). Extrapolation of these growth data to monthly averages suggests that the shallow water extermination occurred in mid-January 1977. Maximum–minimum thermometers on the reef showed that surface waters reached 14°C in the Dry Tortugas on January 21 (19), which correlates well with the cessation of growth measured in the stained shallow water specimens. Reduction in coral skeleton growth rate has been correlated with cold ambient temperatures in the Florida Keys by examination of coral skeleton banding patterns (20) and has been experimentally induced during transplantation experiments with *A. cervicornis* (21).

The Dry Tortugas coral reef community was drastically altered during the winter of 1976–1977. Ninety-six percent of the living coral cover in the survey depths of <2 m died (Fig. 1). As seen in the sample frames, the shallow water *A. cervicornis* suffered tissue death only. The skeletons were fully intact, indicating that death was not induced by physical damage due to storm or wave stress. At the time of sampling, the skeletons supported a thick mixed assemblage of filamentous and fleshy epiphytic algae.

Table 1 shows contrasting coral community changes between shallow and deep water stations. Both stations experienced a reduction in percent cover, but only significantly so in shallow water, where a significant reduction in species number and species diversity also occurred. These parameters did not change ($P < 0.01$) in deep water. However, at both depths, the amount of living coral in close proximity (1–5 cm from each other) decreased significantly.

Acquisition of substrate occurs both by growth involving indirect exploitative means (shading) and direct interference competition (extracoelenteric destruction) as well as by settlement or physical displacement after stochastic events. Because the effects of both shading and extracoelenteric destruction are initiated at the growing edge of a colony, the potential for competitive interactions may be measured in this community by the length of perimeter in proximity to other colonies.† Analysis of perimeter contiguity in the 13-m station reveals a 70% reduction in competitive interactiveness whereas the other parameters failed to show any change at all (Table 1).

These results show that although changes in commonly used community indices—such as species diversity, percent cover, species number, and relative abundance of individual colonies—may be adequate to detect community responses to extreme stresses, the explicit inclusion of relative position with respect to neighboring colonies is necessary to assess the influence played by inter- and intraspecific competitive interactions on community structure and how these influences change significantly during substantial (shallow water) as well as subtler (deep water) perturbations.

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* The entire Tortugas reef tract down to the 20-m-depth contour consists of 3% live coral cover, of which over half is *A. cervicornis* (17).
† As the actual distances between colony perimeters determine whether an interaction will or will not occur, our computer measured this intercolony distance and was arbitrarily programmed to score the length of perimeter at close range (<1 cm) to simulate extracoelenteric destruction and medium range (<5 cm) to include effects such as shading. However, it must be remembered that these photographs compress a three-dimensional system of variable height into two dimensions. The effect of this simplification is to sum the competitive interactions of dominance and shading. Even though both of these competitive abilities have a detrimental effect on the loser, extracoelenteric destruction usually acts faster than shading in tissue destruction.
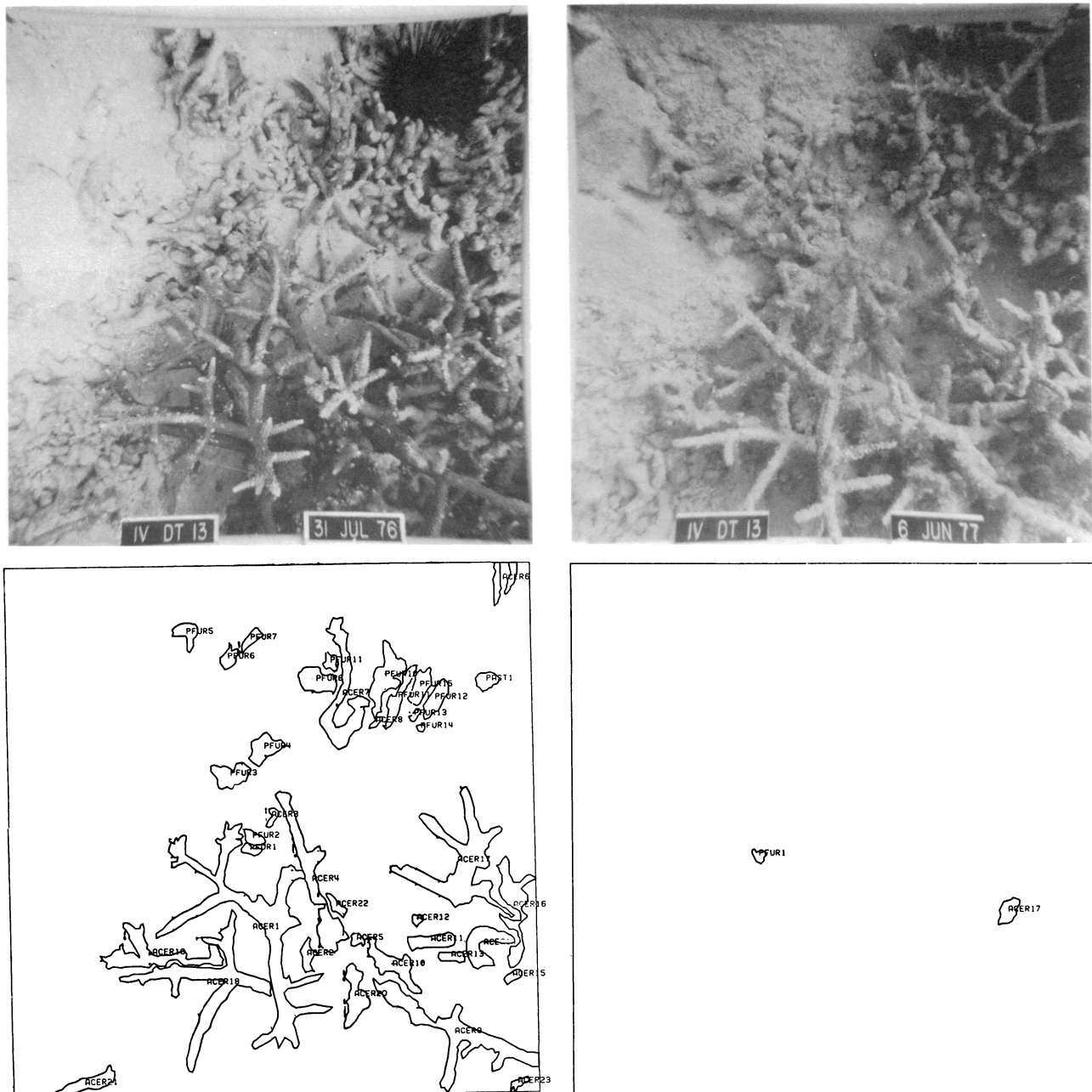
FIG. 1.   Shallow (1.3 m) Dry Tortugas coral reef substrates before (*Left*) and after (*Right*) the severe winter of 1976–1977. (See Fig. 2 for deep coral reef substrates.) Photographs (*Upper*) and their digitized representations (*Lower*) include a 0.5 m × 0.5 m area representative of the community changes (Table 1). Each individual colony larger than 1 cm² is identified to species and its exact locality in the photograph stored on computer for analysis of percent cover, number and relative abundance of species, length of perimeter in proximity to other colonies, spatial relationships within the frame, and occupancy changes between years (16).

The extreme differences in response to temperature stress between shallow and deep communities may be caused by species-specific susceptibility to cold. As predicted by Mayer,[‡] and as corroborated in the photographs, *A. cervicornis* sustained the

‡ Mayer (22), in his examination of the effects of lowered temperature on the survival of Dry Tortugas reef corals, suggests that 14°C constituted lethal conditions for *A. cervicornis*. He reports brief (<1 day) wintertime lowerings of the water temperature to 17.2°C during his 30 yr as laboratory director, but, on the basis of laboratory studies, he makes the following prophetic predictions: "As a result, we are led to conclude that were the water cooled by an exceptionally prolonged norther to 13.9°C for 9 hours, *Siderastrea radians*, *S. siderea*, and *Meandra* (=*Manicina*) *areolata* would survive without injury, while *Porites furcata*, *P. clavaria* (=*divaricata*), *Meandra* (=*Diploria*) *clivosa*, and *Favia fragum* would also survive, but with more or less in-

heaviest mortality.[§] However, species such as *Siderastrea siderea*, *Mycetophyllia ferox*, and *Porites furcata* survived, but with some slight damage, even in shallow water. The relationships between the depth distribution of susceptible species and the depth distribution of lowered temperatures are unknown,

jury, the first-named being the most resistant. On the other hand, this temperature would be fatal to *Obricella* (=*Montastrea*) *annularis*, *Porites astreoides*, and *Madrepora muricata* (=*Acropora cervicornis*)."

§ The only other documented instance of a major cold water kill of Caribbean corals was reported by Verrill (23) for the Bermuda Islands in 1901 when air temperatures dropped to 8°C. Bermuda might be expected to have this kind of disturbance more frequently than southern Florida, and it is interesting to note that the genus *Acropora* is now missing entirely from the Bermuda Archipelago, despite the fact that it is represented there in fossil form.
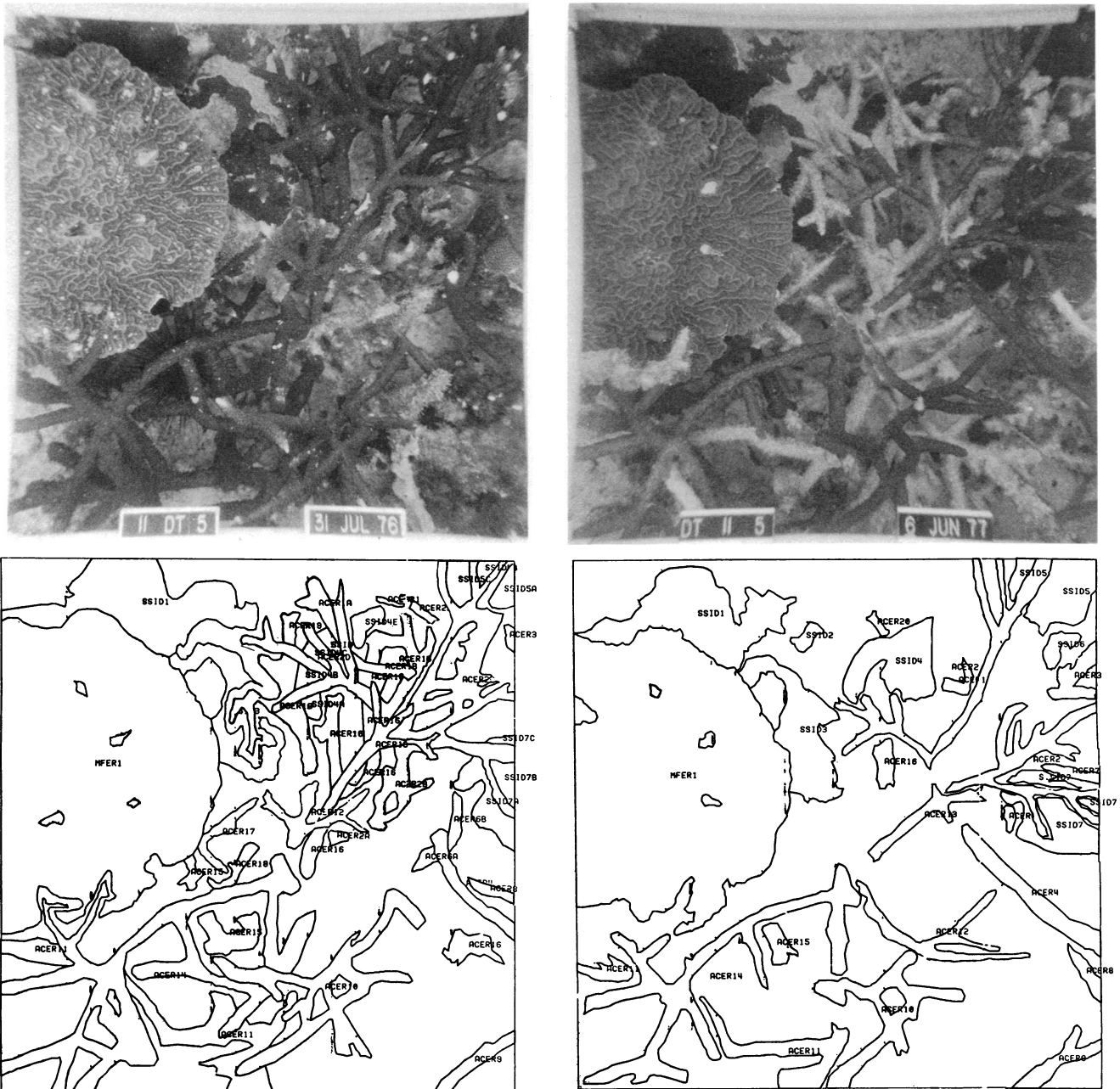
FIG. 2.   Deep (13 m) Dry Tortugas coral reef substrates before (*Left*) and after (*Right*) the severe winter of 1976–1977. (See Fig. 1 for shallow coral reef substrates.) Legend as in Fig. 1.

as only surface temperature recordings are available. However, a smaller percentage of *A. cervicornis* tissue died in the 13-m-deep station, suggesting a reduction in either intensity or duration of the cold stress with depth.

Recovery rates cannot be easily predicted (14) but are being monitored. Where the entire colony has been killed (Figs. 1 and 2), reestablishment of shallow water Tortugas reefs cannot be by asexual regeneration of partially damaged colonies (25, 26)—as appeared to be the case after hurricane damage in the Florida reef tract—but rather must be by settlement of sexually produced planula larvae—as was the case after the Persian Gulf cold-water kill (27).

Recruitment of planulae into the shallow water community may be hindered by the presence of epiphytes and exposed silt and sand substrates (Figs. 1 and 2), which planulae larvae have been shown to avoid (28, 29). Survivorship of the planulae that do settle may be reduced by competition with the algae (30).

Succession within the algal community will lead toward the dominance of crustose coraline algal substrates (31) that are also generally avoided by planulae larvae (28). Therefore, although the intact *A. cervicornis* skeletons will eventually be incorporated into the reef frame, further vertical growth in this region will be retarded due to the lack of living coral and will be dependent upon entrapment and cementation of coral rubble (32). These lower rates will be maintained until reestablishment of an *Acropora*-dominated community.

Despite their existence on the northern fringe of coral reef development (33), coral reefs of the Dry Tortugas are vigorously building atop an underlying Pleistocene fossil reef (32, 34, 35). However, the Pleistocene to Recent section is marked by highly variable rates of carbonate deposition—ranging from 1.91 m to 4.47 m accrued per 1000 yr (34). This range is due primarily to a heretofore unexplained variability in accumulation rate of a primary reef builder, *A. cervicornis*. It seems likely that events

Table 1. Changes in community structure of Dry Tortugas coral reefs, 1976–1977

	Station					
	Shallow (1.3 m)			Deep (13 m)		
	7/31/76	6/6/77	% change	7/31/76	6/6/77	% change
Number of species per frame	1.7 ± 0.8	0.3 ± 0.5	47*	2.6 ± 1.2	2.5 ± 1.2	4†
	(3)	(2)	(33)	(3)	(3)	(0)
Percent cover per frame	51.0 ± 28	2.0 ± 0.7	96*	52.0 ± 22	48.0 ± 21	8†
	(13)	(0.2)	(98)	(54)	(46)	(15)
Species diversity (H', log$_2$) per frame	2.5 ± 0.6	0.7 ± 0.5	72*	2.3 ± 0.18	2.0 ± 0.7	13†
	(3.0)	(0.6)	(80)	(2.6)	(2.5)	(4)
Length, cm per frame						
Conspecific colony perimeters						
Within 1 cm of each other	221 ± 41	30 ± 10	87*	45 ± 11	30 ± 13	33†
	(71)	(0)	(100)	(34)	(16)	(47)
Within 5 cm of each other	885 ± 33	145 ± 23	84*	431 ± 26	121 ± 45	72*
	(234)	(0)	(100)	(503)	(230)	(54)
Interspecific colony perimeters						
Within 1 cm of each other	0.8 ± 1.2	0	100*	41 ± 16	12 ± 8	71*
	(2)	(0)	(100)	(67)	(44)	(41)
Within 5 cm of each other	1.5 ± 3.0	0.2 ± 1.0	99*	521 ± 32	165 ± 45	68*
	(28)	(0)	(100)	(337)	(269)	(20)

Average community parameters ± 95% confidence limits are compiled from the 80 individual photographic frames covering a combined area of 20 m^2 at both the shallow (1.3 m) and deep (13 m) stations on Long Reef, Dry Tortugas, FL. Values are means ± SEM. Numbers in parentheses refer to values from the photographs in Figs. 1 and 2.
* Significance level of $P < 0.01$ or better by t test; $n = 80$.
† Not significant.

such as the one documented here contribute to the growth inconsistencies identified by these geological coring studies.

Ecological models emphasizing the role of disturbance in reducing competitive exclusion during succession (9, 10, 15, 36–38) have received increasing attention as mounting evidence suggests that many environments formerly assumed to be stable received periodic perturbations. Long-term storm records have successfully been used to interpret both normal and abnormal distribution of coral reef benthos (15, 26, 39–41). Because of the fortuitous and unique existence of quantified photographic substrate maps before this event, the data presented here give singularly clear evidence of the profound influence that natural physical disturbance can play in altering patterns of interactions among organisms in a complex community. Standard measures of community structure such as number of species, area coverage, diversity, and relative abundance were insensitive to major changes in competitive interactiveness detected by our perimeter overlap analysis.

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