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The 1998 bleaching event and its aftermath on a coral reef in Belize

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Abstract Widespread thermal anomalies in 1997–1998, due primarily to regional effects of the El Niño–Southern Oscillation and possibly augmented by global warming, caused severe coral bleaching worldwide. Corals in all habitats along the Belizean barrier reef bleached as a result of elevated sea temperatures in the summer and fall of 1998, and in fore-reef habitats of the outer barrier reef and offshore platforms they showed signs of recovery in 1999. In contrast, coral populations on reefs in the central shelf lagoon died off catastrophically. Based on an analysis of reef cores, this was the first bleaching-induced mass coral mortality in the central lagoon in at least the last 3,000 years. Satellite data for the Channel Cay reef complex, the most intensively studied of the lagoonal reefs, revealed a prolonged period of elevated sea-surface temperatures (SSTs) in the late summer and early fall of 1998. From 18 September to 1 October 1998, anomalies around this reef averaged +2.2°C, peaking at 4.0°C above the local HotSpot threshold. In situ temperature records from a nearby site corroborated the observation that the late summer and

early fall of 1998 were extraordinarily warm compared to other years. The lettuce coral, *Agaricia tenuifolia*, which was the dominant occupant of space on reef slopes in the central lagoon, was nearly eradicated at Channel Cay between October 1998 and January 1999. Although the loss of *Ag. tenuifolia* opened extensive areas of carbonate substrate for colonization, coral cover remained extremely low and coral recruitment was depressed through March 2001. High densities of the sea urchin *Echinometra viridis* kept the cover of fleshy and filamentous macroalgae to low levels, but the cover of an encrusting sponge, *Chondrilla* cf. *nucula*, increased. Further increases in sponge cover will impede the recovery of *Ag. tenuifolia* and other coral species by decreasing the availability of substrate for recruitment and growth. If coral populations are depressed on a long-term basis, the vertical accretion of skeletal carbonates at Channel Cay will slow or cease over the coming decades, a time during which global-warming scenarios predict accelerated sea-level rise.

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Introduction

Hurricanes, disease outbreaks, bleaching, and various disturbances and stresses due to human activities have killed corals throughout the Caribbean over the last 25 years (Ginsburg 1994; Williams and Bunkley-Williams 2000; references in Aronson and Precht 2001). At the same time, herbivorous fishes have been reduced on some Caribbean reefs by human exploitation, and the echinoid *Diadema antillarum* experienced >90% mortality from disease throughout the region in 1983–1984 (Hay 1984; Lessios 1988). Coral mortality has in general been followed by the proliferation of fleshy and filamentous (non-coralline) macroalgae, because populations of herbivores have not been able to keep pace behaviorally or numerically with algal growth in the large areas of space opened by the death of corals (Hughes 1994; Steneck 1994; Szmant 1997; Aronson and Precht 2000, 2001; McCook et al. 2001; Williams and Polunin 2001).

Widespread coral bleaching in response to anomalously high summer temperatures has become more frequent since the early 1980s (Glynn 1993; Goreau and Hayes 1994; Hoegh-Guldberg 1999; Williams and Bunkley-Williams 2000; Wellington et al. 2001a). The role of high levels of incident solar radiation in these bleaching events is complex and not well understood (Dunne and Brown 2001; Fitt et al. 2001). Bleaching-induced mass mortalities of corals and other zooxanthellate reef organisms have occurred several times and at a number of localities in the Indo-Pacific, in at least one case leading to the local elimination of two species (Oliver 1985; Glynn 1988; Glynn and de Weerd 1991; Brown and Suharsono 1990; Brown 1997; Wilkinson 2000; Glynn et al. 2001; Riegl 2002). In contrast, bleaching episodes on reefs in the western Atlantic–Caribbean region have until now been followed by recovery of most of the affected coral colonies (Lasker et al. 1984; Porter et al. 1989; Williams and Bunkley-Williams 1990; Lang et al. 1992; McField 1999). In 1997–1998 the highest sea-surface temperatures ever recorded, related to the El Niño–Southern Oscillation (ENSO) and possibly enhanced by global warming (Hansen et al. 1999; Mann et al. 1999; Karl et al. 2000; Lough 2000; Enfield 2001), were associated with severe coral bleaching and subsequent mortality in many areas of the world (Wilkinson et al. 1999; Goreau et al. 2000; Wilkinson 2000; Glynn et al. 2001; Wellington et al. 2001a).

On reefs in the central sector of the Belizean shelf lagoon, positive thermal anomalies during the La Niña phase of the ENSO cycle in 1998 resulted in the most extensive bleaching-related mass mortality of scleractinian corals recorded in the Caribbean to date, with nearly 100% of the coral colonies completely killed by early 1999 (Aronson et al. 2000). Paleoecological records from cores extracted from the Belizean reefs suggest that this mass mortality was unprecedented in at least the last 3,000 years (Aronson et al. 2000, 2002). As with the earlier trends to increased coral mortality elsewhere in the Caribbean, the collapse of coral populations on lagoonal reefs in Belize in 1998–1999 opened extensive areas of substrate for colonization. Unlike the situation on other Caribbean reefs, however, herbivores continued to control macroalgal cover. In this paper we document the thermal conditions in 1998 that led to bleaching on a well-studied reef in the Belizean shelf lagoon, the Channel Cay reef complex. We explore community dynamics during and after the 1998–1999 mass coral mortality, and we discuss the prospects for recovery of affected coral populations and the implications for continued reef accretion.

Study area

The central sector of the shelf lagoon of the Belizean barrier reef system is characterized by numerous atoll-like, diamond-shaped reefs known as rhomboid shoals. The Channel Cay reef complex (16°38'N, 88°10'W; Fig. 1), which is 4 km long and 0.5 km wide at its

widest, is the best-studied of the rhomboid shoals. Several investigators have cored this reef extensively (reviewed in Aronson and Precht 1997), and two of us (R.B.A. and W.F.P.) have been conducting ecological surveys there since 1986. Qualitative observations of the ecology of Channel Cay date to the early 1970s (I.G. Macintyre, personal communication).

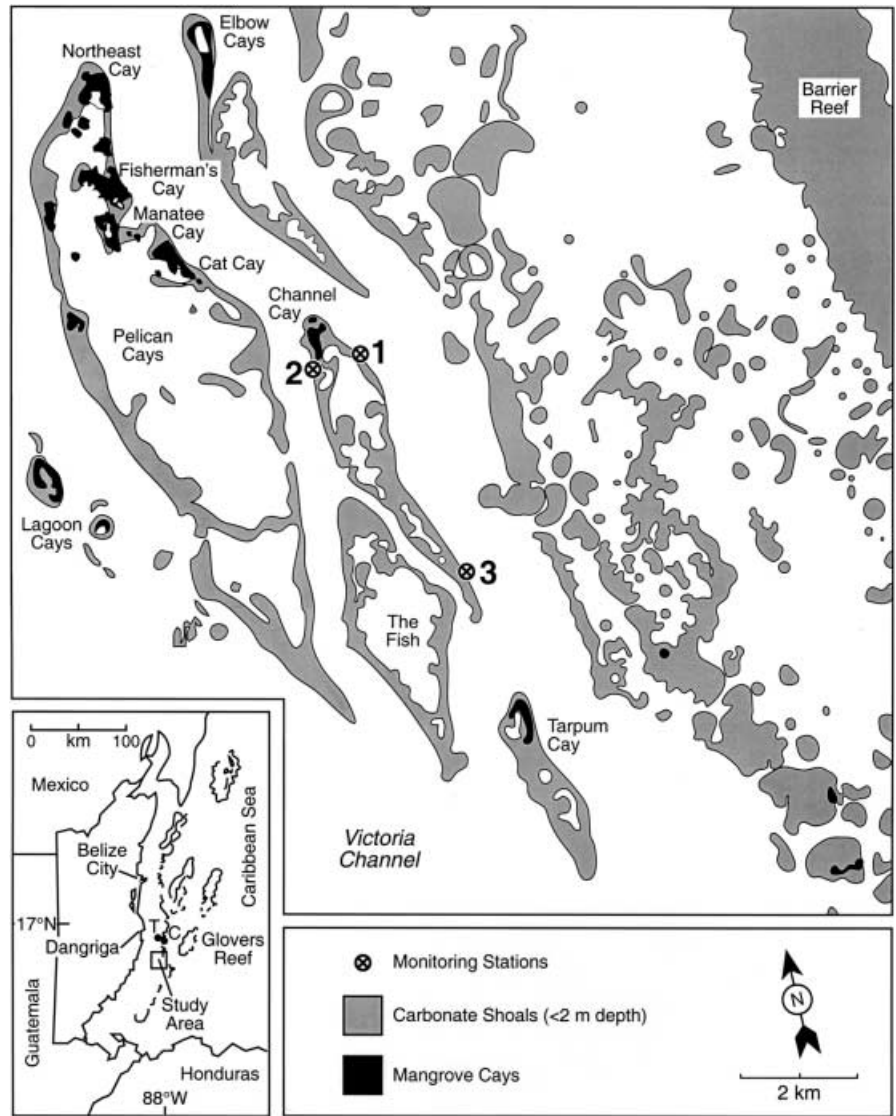
The rhomboid shoals grew to sea level over the last 8,000–9,000 years, following the flooding of the central sector of the Belizean shelf (Precht 1993; Burke 1994; Aronson et al. 1998; Macintyre et al. 2000). The maximum measured vertical accretion rate for Channel Cay, 8 m/1,000 years, is high compared to other Caribbean reefs (Macintyre et al. 1977; Westphall 1986). Because the rhomboid shoals are situated in a low-energy environment, there is little to no submarine cementation (see Purser and Schroeder 1986; Macintyre and Marshall 1988). The Holocene deposits that underlie the living communities consist primarily of interlocking skeletons of the staghorn coral *Acropora cervicornis* packed in fine sediment (Aronson and Precht 1997). Debris fans at the bases of the outer flanks (22–30 m water depth) suggest occasional storm disturbance; however, Hurricane Greta in September 1978, the last major storm in Belize prior to 1998, had no discernible long-term effect on the living community at Channel Cay (Westphall 1986).

Before the late 1980s, the communities inhabiting the outer flanks of Channel Cay and the other rhomboid shoals were dominated by *Ac. cervicornis* (>70% live cover of *Ac. cervicornis* in some places) from 3–15 m depth (Aronson and Precht 1997). *Agaricia tenuifolia* and other species of lettuce coral of the family Agariciidae were subdominant components in that depth range, and they dominated the benthos below 15 m. During the 1980s, white-band disease (WBD) nearly eliminated the *Ac. cervicornis* populations in the shelf lagoon, as well as on the outer barrier reef and in the lagoon at Glovers Reef, an atoll-like carbonate platform seaward of the barrier reef (McClanahan and Muthiga 1998; Aronson and Precht 2001). *Ac. cervicornis* colonies killed by WBD collapsed rapidly, due to the weakening effects of bioerosion.

In the lagoon at Glovers Reef, fleshy and filamentous macroalgae colonized patch reefs formerly occupied by large stands of *Ac. cervicornis* (this also happened in fore-reef habitats at Glovers Reef and along the outer barrier reef; McClanahan 1999; McClanahan et al. 1999). Although regular echinoids, *Echinometra viridis*, were abundant on patch reefs in the lagoon at Glovers Reef, their foraging was severely constrained by predatory fishes (McClanahan 1999). Since herbivorous fishes – parrotfish (Scaridae) and surgeonfish (Acanthuridae) – were not abundant enough to control algal growth, macroalgae came to dominate the patch-reef habitat in the absence of the echinoid *D. antillarum*.

The predators of *E. viridis* that McClanahan (1999) identified at Glovers Reef – triggerfish (Balistidae), the jolthead porgy *Calamus bajonado* (Sparidae), and the hogfish *Lachnolaimus maximus* (Labridae) – were

Fig. 1. Map of the central shelf lagoon of the Belizean barrier reef, showing locations of the sampling stations along the Channel Cay reef complex. Inset map shows location of the study area within the Belizean barrier reef system; *solid circles* show approximate locations of in situ temperature recorders at Carrie Bow Cay (C) and Twin Cays (T)



essentially absent from the rhomboid shoals (<10 *L. maximus* were observed in >100 h of diving during the period 1986–2001). Likewise, herbivorous fishes have been at least two orders of magnitude less common on the rhomboid shoals than in fore-reef habitats along the barrier reef since the earliest observations in the 1970s (I.G. Macintyre, personal communication; R.B.A. and W.F.P., personal observation). As a result, *E. viridis* has been the most abundant herbivore at Channel Cay and the other shoals for decades at least, and it consumed most of the macroalgae that colonized the rubble of dead *Ac. cervicornis* branches after 1986 (Aronson and Precht 1997). *Ag. tenuifolia* and the other agariciids readily recruited to and grew on the *Echinometra*-grazed *Ac. cervicornis* rubble. The cover of *Ag. tenuifolia* increased dramatically, reaching 56% at Channel Cay and as high as 85% at Cat Cay (Fig. 1) by the mid-1990s (Aronson and Precht 1997; Aronson et al. 2000).

Colonies of *Ag. tenuifolia* growing in this lagoonal setting during the 1990s formed assemblies of vertical

blades with an overall inverted-pyramid shape. As they grew 0.5–1 m tall, their high centers of gravity eventually caused them to topple, creating small scree slopes of *Agaricia* rubble. Herbivory by *E. viridis* kept this newly generated coral rubble free of macroalgal growth (<10% cover) at Channel Cay, permitting *Ag. tenuifolia* to recruit continuously at a high rate. Meanwhile, the combined cover of other coral species remained low ($\leq 9\%$ from 1986 to 1998). The *Acropora*-to-*Agaricia* transition occurred throughout the central and southern shelf lagoon in the 3- to 15-m depth range, over an area encompassing hundreds of square kilometers.

Materials and methods

Temperature records

Studies of coral bleaching are increasingly making use of satellite records of water temperature. In many remote oceanic areas, such sea-surface temperatures (SSTs) constitute the sole source of

temperature data, providing valuable time-series perspectives (e.g. Bruno et al. 2001; Mumby et al. 2001). For this study, SST data were sampled from the NOAA/NASA AVHRR (advanced very high resolution radiometer) Oceans Pathfinder archive at 9-km resolution (Best SST Product; Kilpatrick et al. 2001; Toscano et al. in press). Pathfinder 9-km SST data are tuned, via coincident buoy matchups, to in situ bulk SST measurements (top 1 m of the water column; Kilpatrick et al. 2001).

We used the Pathfinder archive to produce a 15-year (1985–1999) record of SSTs for the area surrounding Channel Cay. Interim-version Pathfinder data for 2000 and 2001 were added to complete the time series through 18 August 2001 (K. Kilpatrick, E. Kearns and V. Halliwell, unpublished data). Each datum represents the average, on a daily basis, of combined daytime and nighttime SST data from a 3×3 array of 9-km pixels (an area of 729 km²) centered on the southeastern edge of the Channel Cay reef complex (station 3 in Fig. 1). Gaps in the time series are due primarily to contamination of the data by cloud cover. In each of the pixels used in the spatial average, the SST represents the daily analyzed field, which is the average of all valid satellite SST observations within the 9-km pixel, weighted toward the center. These 9-km data are site-specific to the Channel Cay reef complex, as compared to the 100-km resolution and blended data used by Mumby et al. (2001) to establish the warm-water context for the 1998 bleaching event at Rangiroa Atoll, French Polynesia.

Pathfinder SSTs slightly underestimate temperatures in the upper 1 m of the water column in the tropics (20°S to 20°N), showing a negative bias of ~0.1–0.2°C. In the present case, the Pathfinder SST data were compared to water temperatures measured in situ as part of the Caribbean Coastal Marine Productivity (CARICOMP) Program (CARICOMP 2001). Temperature loggers (Onset Stowaway[®] and TidBit[®]) were deployed in the seagrass beds 75 m west of Carrie Bow Cay (16°48'N, 88°05'W) and 100 m east of Twin Cays (16°50'N, 88°06'W), or ~22 km north of Channel Cay in both cases (Fig. 1). Carrie Bow Cay, a small island in the central sector of the outer barrier reef, is the location of the Smithsonian Institution's field station for the Caribbean Coral Reef Ecosystems program (Rützler and Macintyre 1982). Twin Cays is a complex of two large and four small intertidal mangrove islands in the lagoon approximately 3 km northwest of Carrie Bow Cay. Temperature was recorded at 15- to 48-min intervals, beginning in August 1995 at Twin Cays (1.4 m depth) and in November 1997 at Carrie Bow Cay (2.0 m depth). A break in the Twin Cays temperature record during 1998–1999 resulted from loss of the loggers, due either to Hurricane Mitch (25–31 October) or to theft.

Bleaching thresholds

Bleaching, the loss of algal symbionts and/or their pigments, is a response of zooxanthellate reef organisms to a number of potential stresses. These stresses vary regionally and seasonally, and they may act singly or synergistically to cause corals to bleach (Fitt et al. 2001). The most obvious and most easily documented one is thermal stress. Corals are exposed during local summertime to temperatures near the upper limits of their thermal tolerances (Jokiel and Coles 1990; Glynn 1993; Hoegh-Guldberg 1999). Field and laboratory studies have shown unequivocally that sustained, anomalously high summertime water temperatures are associated with coral reef bleaching; as the magnitude of the thermal anomaly increases, the time required to induce bleaching decreases substantially (Glynn and D'Croz 1990; Podestá and Glynn 1997, 2001; references cited above). Podestá and Glynn (1997) determined that the thermal anomaly must exceed a specific, local threshold value for bleaching to occur; this threshold value lies between the highest locally tolerated, non-bleaching temperature and the lowest temperature known to initiate bleaching in the area. In general, SSTs of ≥1°C above local mean summer maximum temperatures (or prevailing mean summer temperatures), sustained over several weeks, correlate with observed bleaching events (the "hot spots" of Goreau and Hayes 1994; Strong et al. 1997).

HotSpot mapping at 50-km global resolution was initiated in 1997 to establish the historical, climatological maximum monthly

mean (MMM) in every area of the global ocean, so that summer-season thermal anomalies could be computed and mapped on a near-real-time basis (see <http://psbsgi1.nesdis.noaa.gov:8080/PSB/EPS/SST/climohot.html>). HotSpots exceeding the MMMs by ≥1°C were used to predict thermally induced bleaching worldwide during 1997–1998 and thereafter (Toscano et al. in press).

For the present study, HotSpot thresholds were recalculated at 9-km resolution from the combined daytime and nighttime ("Day+Night") Pathfinder data for the pixels covering Channel Cay and, separately, Carrie Bow Cay and Twin Cays. Separate SSTs and threshold values centered on Twin Cays were obtained within the 9-pixel retrieval grid for Carrie Bow Cay, with slight differences in the weighting of pixels leading to small differences in the averaged SSTs and calculated thresholds. The HotSpot thresholds were calculated as the average of Day+Night MMM SSTs over the 9-year baseline period 1985–1993 (Toscano et al. 2002). Bleaching thresholds were set at 1°C above the local HotSpot thresholds. Because data on solar radiation are not available for the study area during the bleaching event, the HotSpot anomalies, bleaching thresholds, and exposure times above threshold temperatures determined for Channel Cay represent the best environmental data available for investigating retrospectively the mass bleaching event of 1998 and the subsequent mortality of reef organisms.

Previous investigators have used only nighttime ("Night") SST data, to avoid potentially high positive biases in daytime ("Day") SSTs (Montgomery and Strong 1995; Wellington et al. 2001b). Our use of daytime and nighttime (Day+Night) Pathfinder values for the Channel Cay area increased the number of available SST measurements by a factor of two over Night data alone. Day+Night data also gave us a more valid basis of comparison with the in situ data, which were collected continuously and are used here as 24-h averages. As a preliminary test of the utility of Day+Night SST data, separate correlation analyses were conducted to compare Pathfinder Day+Night, Day, and Night averages for Carrie Bow Cay to the 24-h in situ means for Carrie Bow Cay. These analyses produced Pearson product-moment correlation coefficients (*r* values) of 0.880, 0.892, and 0.888, respectively (*n* = 797, 548, and 426), all of which were highly significant at *P* < 0.001. In other words, Night SST data from Carrie Bow Cay did not perform appreciably better in comparison with daily means of in situ data than did Day or combined Day+Night SST data. Additional information on the performance of the Pathfinder data can be found in Kearns et al. (2000) and Kilpatrick et al. (2001).

Reef surveys

Benthic surveys were conducted using scuba at stations on the outer flanks of the Channel Cay reef complex. Following Aronson and Precht (1997), corals and other sessile biota were sampled along permanent transects by the linear point-intercept (LPI) method. A fiberglass surveyor's tape was laid along the outer reef slope, perpendicular to the depth contours. A diver swam along the tape identifying and recording the sessile organisms under each 10-cm mark. The primary living constituents were hard corals (Scleractinia and Milleporina), algal turfs, crustose coralline algae, fleshy and filamentous macroalgae, and sponges.

Crustose coralline algae, fine algal turfs (filaments <2 cm tall and so sparse that the substratum is visible), and bare space can be difficult to distinguish and quantify in LPI surveys. These three components were combined into a single category, abbreviated CTB (crustose/turf/bare). The CTB category is an indicator of intense herbivory (Aronson and Precht 2000).

One transect was surveyed at each of three permanent stations at Channel Cay, which were separated by distances of 1–3.5 km (Fig. 1). The transects, which were marked with flagging tape, were approximately 20 m long and spanned 3–15 m depth. The three transects were surveyed in December 1996, August 1997, October 1998, January, March, June, and October 1999, February 2000, and March 2001.

Densities of juvenile corals were estimated at 9 and 15 m depth at the permanent stations in June 1994 (when the cover of

Ag. tenuifolia was ~50%; Aronson and Precht 1997), March 1999, February 2000, and March 2001. At each depth at each station, 0.25-m² quadrats were positioned haphazardly along the depth contour, within 50 m of the transect line on either side. Juvenile corals (≤ 5 mm in longest dimension with smooth, regularly shaped margins) were counted visually with the aid of an underwater flashlight (Edmunds et al. 1998). Echinoids, which were almost exclusively *E. viridis*, were counted in the quadrats at the same time as juvenile corals. Stations 1 and 2 were sampled in 1994 with 51 quadrats at each depth at each station. Station 3 was added for the 1999–2001 counts, and 25 quadrats were sampled at each depth at each station during each visit.

Statistical analysis of survey data

The transect data were expressed as percent covers of the various substrate components for graphical representation and as proportional covers for statistical analysis. Repeated-measures analysis of variance (ANOVA) was used to compare the proportional covers of individual substrate components among sampling dates. Four components were tested in separate, univariate analyses: hard corals, macroalgae, CTB, and sponges. A randomized, complete-block design was used, in which the stations (i.e. the transects) were the blocks and survey date was the fixed factor (see Aronson and Precht 1997). The assumptions of parametric statistics, normality and homogeneity of variances, could not be tested because the data were unreplicated within stations and sampling dates. As a precaution, however, the proportional cover data were arcsine-transformed prior to ANOVA.

Our approach to hypothesis-testing conformed to the Model 2 blocked design of Newman et al. (1997): the stations were established arbitrarily so block \times factor interactions were assumed not to have occurred. Using this model, however, the conclusions drawn were necessarily limited to the particular transects surveyed. Newman et al. (1997) discuss the complexities of blocked designs.

ANOVAs and a posteriori pairwise comparisons were computed using the SYSTAT[®] 8.0 statistical package. Critical values for significance testing in the ANOVAs were adjusted to control experimentwise error. We used the Bonferroni procedure and more powerful sequential Bonferroni and Dunn–Šidák procedures (Rice 1989; Winer et al. 1991) to adjust the α levels to the number of *F*-tests performed. Since the four components of substratum cover were not independent, the significance tests were not independent; however, none of these adjustment procedures requires independence of the tests. The three procedures yielded the same results.

A similar approach was used to analyze the quadrat data. Counts from the quadrats were pooled to obtain mean estimates of the abundance of juvenile corals and, separately, the abundance of *E. viridis* for each depth at each station in each survey year. Among-station means and standard errors for each depth and survey year were calculated from those within-station means. The pooled data, expressed as counts of juvenile corals (or *E. viridis*) per quadrat, were analyzed using a Model 2 randomized, incomplete-block ANOVA design, with the stations considered as blocks, and depth and survey date treated as fixed factors. The addition of a third station after the 1994 survey did not alter patterns of abundance of juvenile corals and *E. viridis* in time or with depth.

As with the transect data, it was not possible to test for conformity of the pooled count data to the assumptions of parametric statistics. According to the central-limit theorem, however, these pooled counts within stations and times should be normally distributed, since they represent the means of replicate quadrats. Despite this reasonable expectation of normality, count data often do not conform to the assumption of homogeneity of variances. To minimize this problem the data were logarithmically transformed prior to ANOVA.

Significance tests for the quadrat data were again based on adjusted α levels. The densities of juvenile corals and *E. viridis* may not have been independent, since grazing by *E. viridis* is known to promote coral recruitment (Sammarco 1982). Again, the adjustment procedures do not require the statistical tests to be independent.

Results

Temperature records

The Pathfinder data (Fig. 2A) show elevated SSTs at Channel Cay from 3 August through 9 October 1998. Mass bleaching was first observed on the rhomboid shoals in early September 1998 (Bright and McField 1998; Nemecek 1999), in the middle of this prolonged period of high SSTs. As discussed in Materials and methods, the Pathfinder SSTs are likely to be slight underestimates of temperatures in the upper 1 m of the water column.

In August 1998, SSTs exceeded the Channel Cay HotSpot threshold of 29.77°C for 7 days, in 2-day peaks. These peaks were interrupted by 6- to 8-day intervals of no data and drops of 0.07–1.5°C below the HotSpot threshold, both of which were due to cloudy conditions. From 2 September to 9 October, SSTs exceeded the 29.77°C threshold for 13 of the 17 days for which satellite SSTs are available. During September, positive anomalies of 0.83°C and higher (above the HotSpot threshold) occurred singly and in several 2- to

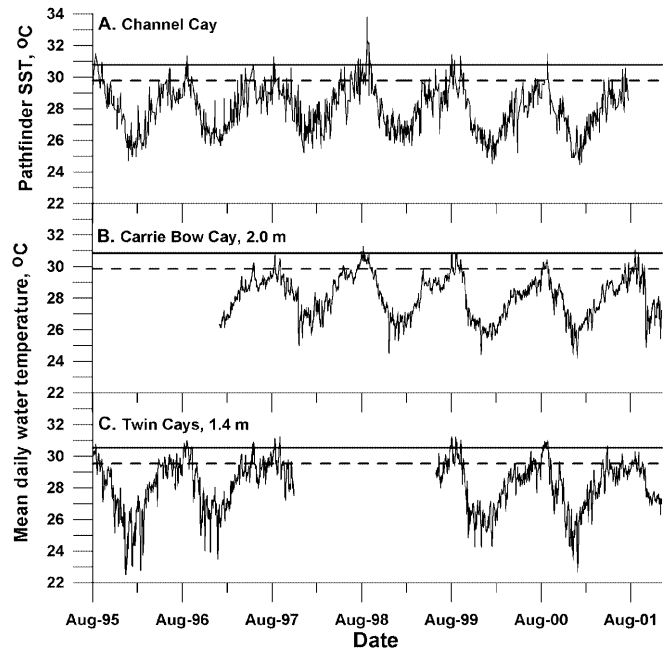


Fig. 2A–C. Temperature records from the central sector of the Belizean barrier reef. A Pathfinder 9-km SST for Channel Cay (all available daytime and nighttime SSTs combined). The HotSpot threshold (29.77°C) is shown by the dashed line; the bleaching threshold (HotSpot threshold + 1°C, or 30.77°C) is shown by the solid line. B In situ mean daily water temperature at Carrie Bow Cay, 2.0 m depth. HotSpot (29.85°C) and bleaching (30.85°C) thresholds, derived from Pathfinder SST measurements centered on Carrie Bow Cay, are denoted by dashed and solid lines as in A. C In situ mean daily water temperature at Twin Cays, 1.4 m depth. HotSpot (29.55°C) and bleaching (30.55°C) thresholds, derived from Pathfinder SST measurements centered on Twin Cays, are denoted as in A.

3-day clusters. Anomaly levels increased from the +1.0°C level during 2–14 September, then peaked during 18, 19, and 20 September at +2.2°C, +4.0°C, and +2.5°C. Five days later, during 26 September to 1 October, positive anomalies ranged from 0.83 to 2.4°C over a 6-day period.

The daily averages of Pathfinder SST for Channel Cay were highly correlated with the daily averages of in situ water temperature measured at Carrie Bow Cay (Pearson correlation coefficient, $r=0.872$, $n=807$, $P<0.001$) and Twin Cays ($r=0.847$, $n=615$, $P<0.001$). Mean daily water temperatures measured in situ at Carrie Bow Cay and Twin Cays ranged from 22.5–31.3°C at 1.4–2.0 m depth during 1995–2001 (Fig. 2B, C). The highest recorded temperatures, in terms of maxima and duration, occurred in 1998. During the 4-month (124-day) period from 11 June to 11 October, there were considerably more days in 1998, compared to other years, during which mean daily water temperatures measured in situ at Carrie Bow Cay exceeded the local, Pathfinder Hotspot threshold of 29.85°C (Table 1). There were also more days during which mean daily water temperatures at Carrie Bow Cay exceeded the bleaching threshold (i.e., were $\geq 1^\circ\text{C}$ above the HotSpot threshold). Pathfinder SSTs peaked on 19 September at 32.73°C for Carrie Bow Cay and 33.82°C for Channel Cay. Annual extremes in water temperature are expected to increase shoreward from the barrier reef, explaining the higher maximum SST at Channel Cay.

In summary, positive SST anomalies at Channel Cay fluctuated around the 1°C level from mid-August through early September, possibly initiating the bleaching event. SSTs peaked during an interval of continuous data from 13 to 19 September, and the rate of increase was a rapid 0.62°C per day. This interval could well have been the cause of the greatest physiological stress, leading to the mass coral mortality described in the next section.

Benthic surveys

Surveys at Channel Cay on 22 October 1998 revealed that virtually all living coral colonies were bleached white from 1 m depth down to the base of the reef at

Table 1. Number of days within the 4-month (124-day) period from 11 June to 11 October during which average temperatures recorded in situ at Carrie Bow Cay (2 m depth) exceeded the local Pathfinder HotSpot and bleaching thresholds of 29.76°C and 30.76°C, respectively

Year	Number of days in interval above threshold	
	HotSpot	Bleaching
1997	18	0
1998	63	4
1999	32	1
2000	22	0
2001	25	2

22 m. Complete bleaching was observed in all colonies of *Ag. tenuifolia* at all depths, as well as in almost all colonies of plate-forming agariciids and massive coral species, which were abundant in deeper water (15–21 m). Some of the *Ag. tenuifolia* had already died by October 1998 (Fig. 3); these dead skeletons were free of coral tissue, fresh-looking, unencrusted, and standing in growth position at that time, suggesting recent mortality. Subsequent monitoring revealed that the remaining *Ag. tenuifolia* experienced $\sim 100\%$ mortality between October 1998 and January 1999. The other coral species were nearly eliminated as well, and the total cover of living hard corals dropped nearly to zero (Fig. 3).

A few fragments of massive and plating coral colonies survived in deeper water (≥ 15 m), but coral cover remained low at Channel Cay at all depths for more than 2 years following the bleaching episode. There were no signs of recovery as late as March 2001. A randomized complete-block ANOVA showed a significant effect of survey date on the cover of hard corals ($P<0.0005$; Table 2), and a posteriori pairwise comparisons using the Tukey HSD procedure showed that coral cover was significantly higher in surveys up to and including October 1998 than it was after that date. There was also a significant effect of block (i.e., station).

The cover of macroalgae remained low during the study period, even after coral cover was reduced nearly to zero (Fig. 3; Table 2). Macroalgal cover did not vary significantly through time when the significance level α was adjusted to control experimentwise error ($P=0.057$); however, the low P value indicates some degree of temporal fluctuation. In contrast, the cover of CTB and sponges varied significantly among surveys

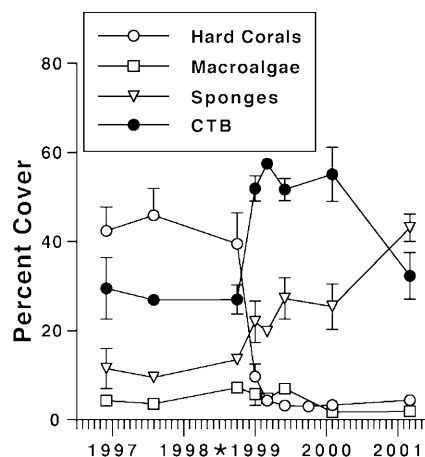


Fig. 3. Changes in benthic cover at Channel Cay. Points represent the among-station means and error bars represent standard errors. In some cases only positive or negative errors are shown for clarity of presentation; absence of error bars indicates that the error was too small to appear on the graph. The asterisk on the abscissa marks the onset of high-temperature anomaly in August 1998. Hard corals include Scleractinia and Milleporina, the latter of which always constituted $<< 1\%$ cover. Virtually all living coral colonies in October 1998 were completely bleached. CTB denotes crustose coralline algae, fine algal turfs, and bare space combined

($P < 0.0005$; Table 2). CTB increased significantly after October 1998, and then it dropped from February 2000 to March 2001 to a level that was not significantly different from pre-bleaching levels (based on Tukey comparisons).

Sponges also varied significantly through time ($P = 0.001$; Table 2). The cover of sponges increased from October 1998 to February 2000, although not monotonically and not significantly (Fig. 3; Tukey comparisons). From February 2000 to March 2001, however, sponge cover increased from 25% to 43%. The cover of sponges in March 2001 was significantly higher than in all surveys prior to June 1999, with the exception of January 1999 (Tukey comparisons). The sponge component of benthic cover consisted almost entirely of an encrusting species, the chicken liver sponge *Chondrilla* cf. *nucula*. This sponge was increasing on the rhomboid shoals prior to 1998, despite high abundances of spongivorous fishes (especially the gray angelfish *Pomacanthus arcuatus*; Rützler et al. 2000; Wulff 2000). The space provided by the mass mortality of corals apparently accelerated this trend, presumably by providing

substrate for encrustation. The drop in cover of CTB from March 2000 to February 2001 was a consequence of the large increase in the cover of sponges. There were no significant block (station) effects for macroalgae, CTB, or sponges after adjustment of the α levels, but the low P value for CTB (Table 2) indicates some variation among stations. Other colonial invertebrates, such as zoanths, ascidians, and encrusting gorgonians, were rare prior to 1998, and their cover remained low through March 2001 (< 2% cover).

Juvenile corals were more abundant at Channel Cay in 1994 than at sites elsewhere in Florida and the Caribbean (Edmunds et al. 1998). At that time, most of the juveniles at Channel Cay were agariciids (Table 3) and most of those agariciids were *Ag. tenuifolia*. Qualitative observations indicate that juveniles remained abundant through December 1997. In October 1998, living juvenile colonies still appeared to be abundant, but all those observed were bleached white.

A randomized incomplete-block ANOVA revealed significant effects of survey year and depth on the abundance of juvenile corals from 1994 to 2001

Table 2. Randomized, complete-block ANOVAs for the cover of hard corals, macroalgae, sponges, and CTB. Proportional data were arcsine-transformed prior to computation of the ANOVAs. Significance tests for block (station) effects assume no block \times date interactions. * significant after adjustment of α to control experimentwise error using Bonferroni, sequential Bonferroni, and Dunn-Sidak procedures

Source	SS	df	MS	F	P
Hard corals					
Block	0.057	2	0.028	8.894	0.003*
Survey date	1.518	8	0.190	59.230	< 0.0005*
Error	0.051	16	0.003		
Macroalgae					
Block	0.001	2	0.0005	1.184	0.834
Survey date	0.072	7	0.010	2.649	0.057
Error	0.054	14	0.004		
Sponges					
Block	0.003	2	0.0015	0.208	0.814
Survey date	0.367	7	0.052	7.820	0.001*
Error	0.094	14	0.007		
CTB					
Block	0.037	2	0.019	5.468	0.018
Survey date	0.399	7	0.057	16.677	< 0.0005*
Error	0.048	14	0.003		

Table 3. Familial composition of juvenile hard corals (Scleractinia and Milleporina) observed in surveys at Channel Cay. Data from all stations at both depths are pooled for each survey; 51 m² total were surveyed in 1994 and 37.5 m² total were surveyed in 1999–2001. Data are not normalized to area, as they are in Fig. 4

Family	Frequency of juveniles in survey (percentage)			
	Jun 1994	Mar 1999	Feb 2000	Mar 2001
Anthozoa: Scleractinia				
Agariciidae	1153 (83.7%)	51 (53.7%)	73 (56.2%)	120 (57.7%)
Poritidae	71 (5.2%)	14 (14.7%)	2 (1.5%)	15 (7.2%)
Mussidae	50 (3.6%)	10 (10.5%)	9 (6.9%)	14 (6.7%)
Pocilloporidae	45 (3.3%)	3 (3.2%)	13 (10.0%)	15 (7.2%)
Faviidae	30 (2.2%)	8 (8.4%)	14 (10.8%)	17 (8.2%)
Astrocoeniidae	11 (0.8%)	3 (3.2%)	4 (3.1%)	13 (6.3%)
Siderastreidae	6 (0.4%)	5 (5.2%)	8 (6.2%)	10 (4.8%)
Caryophylliidae	5 (0.4%)	1 (1.1%)	7 (5.4%)	3 (1.4%)
Meandrinidae	1 (0.1%)	0 (0.0%)	0 (0.0%)	1 (0.5%)
Hydrozoa: Milleporina				
Milleporidae	5 (0.4%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Total	1377	95	130	208

Table 4. Randomized, incomplete-block ANOVAs for the densities of juvenile corals and *Echinometra viridis*. Count data were logarithmically transformed prior to ANOVA. Significance tests for block (station) effects assume no block×factor interactions. * Significant after adjustment of α to control experimentwise error using Bonferroni, sequential Bonferroni, and Dunn–Šidák procedures

Source	SS	df	MS	F	P
Juvenile corals					
Block	0.241	2	0.120	3.186	0.078
Survey year	5.840	3	1.947	51.493	<0.0005*
Depth	2.967	1	2.967	78.481	<0.0005*
Survey year×depth	0.235	3	0.078	2.068	0.158
Error	0.454	12	0.038		
<i>Echinometra viridis</i>					
Block	0.111	2	0.056	1.938	0.186
Survey year	0.445	3	0.148	5.172	0.016
Depth	0.154	1	0.154	5.373	0.039
Survey year×depth	0.141	3	0.047	1.639	0.233
Error	0.344	12	0.029		

(Table 4). By March 1999 juvenile coral colonies, especially agariciids, had experienced catastrophic mortality, dropping in density by approximately an order of magnitude (Table 3; Fig. 4). Tukey comparisons showed that the abundance of juveniles was significantly greater in June 1994 than after 1998, but that the three post-1998 surveys were statistically indistinguishable. Juvenile corals were also significantly more abundant at 15 m than at 9 m. The density of juveniles increased nonsignificantly at 15 m depth from March 1999 to March 2001, but agariciids did not increase disproportionately. They remained rare at 9 m depth through March 2001. There was no block effect, nor was there a survey year×depth interaction (Table 4).

E. viridis was essentially the only species of sea urchin observed in the quadrat censuses from 1994 through 2001, comprising >99% of the echinoid counts. Compared to their abundances in fore-reef habitats, herbivorous fishes were uncommon at Channel Cay, and predators of sea urchins were rare to absent during the study period (see Introduction, Study area). *E. viridis* remained abundant and in fact increased over levels observed in June 1994 (Fig. 5). There were no effects of block, survey year, or depth on the density of *E. viridis* when the α levels were adjusted, although survey year

and depth were nearly significant (Table 4). There was also no significant survey year×depth interaction.

As with the block effect on the cover of CTB, the marginal lack of significant effects of survey year and depth on echinoid density is probably due to low statistical power. Whether or not these effects are significant does not alter conclusions about the dynamics of the reef community at the three stations. The salient point is that the density of herbivores did not decline during the study period.

Hurricane Mitch, a category-5 hurricane, directly struck the Bay Islands of Honduras to the south of Channel Cay on 25–31 October 1998. Hurricane Keith, a category-4 storm, directly struck the northern sector of the Belizean barrier reef on 1–3 October 2000. Storm waves produced by these hurricanes had negligible impacts on the physical structure and sessile organisms of the Channel Cay reef, other than possible minor slumping at the shallowest depths (2–5 m), observed after Hurricane Keith.

Hurricane Iris, a category-4 storm, struck the central and southern barrier reef in early October 2001, after this study was completed. The eye of the storm passed 15–17 km to the south of Channel Cay and hurricane-force winds extended ~25 km from the eye, placing the

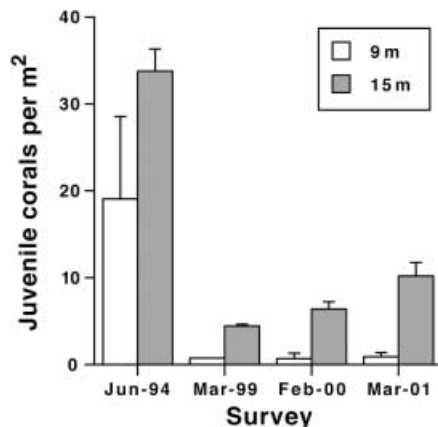


Fig. 4. Changes in the abundance of juvenile corals at Channel Cay. Data are expressed per square meter. Error bars represent positive standard errors; absence of error bars indicates that the error was too small to appear on the graph

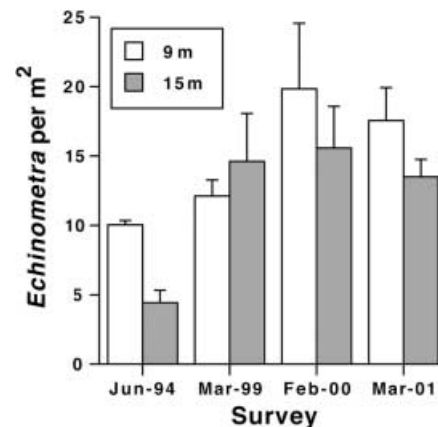


Fig. 5. Changes in the abundance of the sea urchin *Echinometra viridis* at Channel Cay. Data are expressed per square meter. Error bars represent positive standard errors

Channel Cay reef complex within the more damaging northern sector of the cyclone. The effects of Hurricane Iris varied with exposure to storm waves, which came from the east-northeast over the barrier reef crest and into the central lagoon. Preliminary observations in November 2001 suggest that some reworking, scour, and winnowing of sediment occurred on the windward flank of the Channel Cay shoal down to 8–9 m depth (Stations 1 and 3). On the leeward flank (Station 2), sand and some coral heads were brought from the narrow platform at the top of the reef down to 7–8 m depth. The latter effect was strongly attenuated in the lee of the islands that comprise Channel Cay itself. Storm damage reversed the spread of *C. cf. nucula* in some exposed areas, if only temporarily.

Discussion

The first records of widespread bleaching along the Belizean barrier reef coincided with unusually high sea temperatures in the summer and fall of 1995 (Gleeson and Strong 1995; Koltjes et al. 1998). Most of the coral colonies that bleached on the outer barrier reef and offshore platforms during this episode recovered once temperatures declined (Koltjes et al. 1998; McField 1999). At Channel Cay, the mean cover of living corals at the three stations declined from 60% in July 1995 to 42% in December 1996, but then increased to 46% in August 1997 (Figure 9.4 in Aronson and Precht 2001).

In 1998, Channel Cay experienced a prolonged period of higher-than-threshold SSTs, including intervals above the HotSpot and bleaching thresholds. Although gaps in the remotely sensed time series due to clouds make it impossible to account entirely for the variability in the SST data over these intervals, it is apparent that in 1998, particularly from late August through early October, SSTs were consistently elevated to a level sufficient to induce and sustain bleaching, as well as to cause eventual coral mortality. In situ measurements also indicate anomalously high water temperatures in 1998, sustained longer than in previous or succeeding years.

Because bleaching did not occur in 1996 or 1997 (and almost all the corals were already dead by 1999), we can conjecture that bleaching in the Channel Cay area in 1998 was forced by +1°C anomalies (above the HotSpot threshold) established from mid-August through early September, followed by rapidly increasing SSTs – peaking at a +4°C anomaly level – over a relatively short, 8-day period. The period from 18 September to 1 October included 7 days (of 8 for which SSTs were obtained) with SSTs exceeding the bleaching threshold by 0.8–3.1°C; these bleaching levels were apparently maintained across a 5-day, no-data interval. Although the clusters of high anomalies were interspersed with 1- to 5-day periods of no data (due to clouds), the absence of fluctuations below the HotSpot threshold or even reduced positive anomalies in each successive warm interval argues for continued warmth over these cloudy

intervals, and hence sustained positive anomalies over the 23-day period from 14 September to 6 October. The in situ data for Carrie Bow Cay and Twin Cays show the same patterns over the years, with a prolonged period above the HotSpot threshold at Carrie Bow Cay in 1998, and presumably at Twin Cays as well (since the SSTs for Twin Cays were derived from the same retrieval grid that encompasses Carrie Bow Cay).

Although we cannot discount other factors, moderate to high water turbidity and the broad depth range of the ecological effects suggest that elevated temperature was primarily responsible for bleaching in 1998 and subsequent coral mortality. The lack of a depth gradient in the occurrence of bleaching suggests that increased solar radiation was not the principal cause, although it may have contributed to bleaching in the shallower depths (see, e.g., Mumby et al. 2001). Another possible explanation for the mass coral mortality is input of fresh water, sediment, and nutrients to the lagoon following Hurricane Mitch, a storm that caused massive rain-induced flooding along parts of the Central American coast (Guiney and Lawrence www.nhc.noaa.gov/1998mitch.html; see McClanahan et al. [2001] on the possible influence of nutrient-laden, fresh water from Hurricane Mitch at Glovers Reef). Storm-associated runoff created a low-salinity lens that was at least 3 m thick and persisted for at least 3 weeks at Carrie Bow Cay (K.H. Koltjes, personal observation). The broad depth range of effects and the fact that the mass mortality was underway prior to Hurricane Mitch exclude fresh water as the primary cause, although the low-salinity lens could have had some impact in shallow water.

Mass bleaching occurred in fore-reef and back-reef/lagoonal habitats of the barrier reef and offshore platforms during the summer and fall of 1998, but there were no reports of subsequent bleaching episodes through March 2001. Bleaching in 1998 caused some coral mortality in fore-reef habitats throughout Belize and on patch reefs in the lagoon of Glovers Reef (Kramer et al. 2000; McClanahan et al. 2001), but most adult and juvenile colonies recovered their coloration in the months following Hurricane Mitch (Mumby 1999). The primary cause of mortality of *Ag. tenuifolia* on the seaward margin of Glovers Reef was physical damage by waves associated with the hurricane rather than bleaching; those populations have been recovering steadily since then (P.J. Mumby, personal communication). In contrast, coral populations in the central sector of the Belizean shelf lagoon registered catastrophic mortality as a result of the 1998 bleaching event. This was the first bleaching-related mass coral mortality observed in the Caribbean, and it was a novel event on a time scale of millennia.

The subsequent changes in benthic composition at the three stations monitored in this study were representative of patterns observed along the outer flanks of the Channel Cay reef complex and elsewhere in the central lagoon. Catastrophic coral mortality and the failure of coral recruitment occurred after the bleaching

episode of 1998. Following the mass mortality of corals, grazing by the sea urchin *E. viridis* limited the growth of macroalgae on the dead coral surfaces. This apparently enabled the encrusting sponge *C. cf. nucula* to increase opportunistically. Qualitative and quantitative observations on other rhomboid shoals revealed that the timing of post-bleaching dynamics varied to some extent among locations. The overall pattern, however, was essentially the same throughout an area of at least 375 km².

Predicted effects of global climate change on coral reefs include dramatically increased coral mortality due to bleaching and emergent diseases, as well as decreased rates of reef accretion (Smith and Buddemeier 1992; Glynn 1993, 1996; Harvell et al. 1999; Kleypas et al. 1999; Lough 2000). The ecological dynamics of the reef at Channel Cay (and the other rhomboid shoals in the central lagoon) appear to bear out these predictions. The near-elimination of one dominant coral species (*Ac. cervicornis*) by white-band disease, its opportunistic replacement by another coral (*Ag. tenuifolia*), and the near-elimination of the second dominant coral species by bleaching were unprecedented events on a time scale of millennia (Aronson and Precht 1997; Aronson et al. 2000), and they followed several millennia of stable sea level (~1 m sea-level rise in Belize over the last 3,000 years; Macintyre et al. 1995). Like intertidal and subtidal communities in other parts of the world, the trajectory of this reef community is strongly influenced by rare, rapid, extreme events (e.g., Gaines and Denny 1993), although it is possible that a more gradual deterioration of environmental conditions in the Caribbean predisposed the biota to sudden and radical shifts in dominance (Nyström et al. 2000).

It is unlikely that *Ac. cervicornis* will recover on the rhomboid shoals in the near future. Since this species reproduces primarily by fragmentation, its potential for recolonization is low following removal from a large area (Knowlton 1992). *Ag. tenuifolia*, in contrast, possesses life-history characteristics that favor its colonization of disturbed reef surfaces. This species is eurytopic in terms of habitat preference and grows rapidly in the central lagoon under a broad range of light and flow conditions (Helmuth et al. 1997a, b; Shyka and Sebens 2000). It also reproduces by brooding internally fertilized planula larvae (Morse et al. 1988), a trait that enables it to recruit locally and preempt space following disturbances (e.g., Smith 1992). On the other hand, *Ag. tenuifolia* is particularly prone to temperature-induced bleaching (Lasker et al. 1984; McField 1999; Shulman and Robertson 1996).

If the herbivorous activities of *E. viridis* continue to control the cover of macroalgae, then *Ag. tenuifolia* could reestablish itself in the central lagoon, possibly increasing initially at depths ≥ 15 m and then spreading to shallower water. The continued rapid growth of *C. cf. nucula*, however, is likely to exclude *Ag. tenuifolia* and other corals from much of the newly opened space. This chondrillid sponge grows rapidly in a variety of reef

habitats, and it may deter predatory angelfishes (Pomacanthidae) – of which there are large populations on the rhomboid shoals – by means of chemical defense (Swearingen and Pawlik 1998). Vicente (1990, 1994) concluded that *C. cf. nucula* was the most aggressive competitor for substratum on reefs in Puerto Rico, where it overgrew most coral species and other types of sessile benthos. Suchanek et al. (1983) also found the species to be among the most aggressive in St. Croix, U.S. Virgin Islands. On the other hand, Aerts (1998) found *C. cf. nucula* to be less aggressive on reefs in Curaçao and Colombia. On those reefs it was more successful where coral cover was lower. Our data from the rhomboid shoals in Belize also suggest that this sponge is primarily opportunistic, taking advantage of the space opened by coral mortality.

Increased monopolization of substrate on the rhomboid shoals by *C. cf. nucula* will reduce coral recruitment by preventing planulae from settling. Under such circumstances, bioerosion of dead coral skeletons should continue apace or increase on those reefs, as it did after the WBD outbreak in the late 1980s (Aronson and Precht 1997). If corals are unable to recover substantially, vertical accretion will be slowed or possibly arrested over the next several decades, at a time when sea-level rise is expected to accelerate due to global warming. It is entirely possible that the reefs at Channel Cay and the other rhomboid shoals will lag behind rising sea level over the next few centuries, degrading from the catch-up/keep-up reefs they have been for the past 8,000–9,000 years (Precht 1993; Burke 1994; Aronson et al. 1998; Macintyre et al. 2000) to incipiently drowned shoals or give-up reefs (Kendall and Schlager 1981; Neumann and Macintyre 1985; Graus and Macintyre 1998).

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