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The recent collapse of a rapid phase-shift reversal on a Jamaican north coast coral reef after the 2005 bleaching event

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Abstract: The community structure of most Caribbean reefs has changed dramatically since the 1980s. Invoking a chemistry analogy, in 1994 Hughes termed the change a "phase shift" to describe the change from a coral dominated habitat to one dominated by macroalga on the north coast of Jamaica over a period of 17 years. The loss of live coral cover is exemplified by the demise of *Acropora* spp. in Discovery Bay, Jamaica. Dense, monospecific high relief thickets of *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral) were characteristic of shallow and intermediate depth coral communities in the Caribbean prior to the late 1970s. In the early 1980s, *A. cervicornis* live coral cover was >21% at several sites around Discovery Bay, by 1987 it had declined to less than 1%. No large population of *Acropora* reestablished in the vicinity of Discovery Bay for nearly two decades. In 1995, *A. cervicornis* cover at Dairy Bull Reef (DBR) was only 0.6%. By 2004, *A. cervicornis* cover had increased to about 10.5% . In 2005, *A. cervicornis* cover further increased to 44%. This increase in *A. cervicornis* cover was part of the important "phase shift reversal" reported by Idjadi *et al*. in 2006. An isolated population of *A. cervicornis* exhibited similar coral cover at East Rio Bueno (ERB). In 2005, both populations of *A. cervicornis* bleached; however, the two populations responded differently. The population at DBR was decimated by the bleaching event and the surviving remnants were attacked by *Coralliophila*. At DBR, cover declined to <0.5% by June 2006. The population at ERB recovered from the bleaching event with little decrease in cover. Coral recruitment was examined over three spawning periods on DBR. Only two *Acropora* spat recruited to settlement tiles – one in 2003 and one in 2005. *Acropora* recruitment represented only 0.7% of the total spat recruiting to the tiles during the entire sampling period. Rev. Biol. Trop. 56 (Suppl. 1): 149-159. Epub 2008 May 30.

Key words: *Acropora cervicornis*, restoration, recruitment, planulae.

Four decades ago Goreau and Goreau (1973) documented Caribbean coral reef community structure on north coast Jamaican reefs. The importance of their studies became increasingly recognized as shallow water live coral cover declined throughout the region and the acroporids became locally extinct on many reefs (Knowlton *et al.* 1990). In fact, their work was used as a standard by which coral reefs were measured throughout the Caribbean.

Prior to 1980, *Acropora cervicornis* was abundant at the West Fore Reef at Discovery Bay (Goreau and Wells 1967, Tunnicliffe 1983). However, in the 1980's, the cover of *A. cervicornis* was reduced from 53% ± 10% to a negligible presence by Hurricanes Allen (1980) and Gilbert (1988) (Woodley *et al.* 1981, Crawford 1995, Woodley 1991). Recovery of *A. cervicornis* after Hurricane Allen was impeded by high mortality of surviving fragments caused by disease (Knowlton *et al*. 1981). During the past 25 years, there has been no wide – spread increase in *A. cervicornis* due to disease and predation (Bruckner *et al*. 1997) and the low rate of sexual recruitment characteristic of this species (Sammarco 1980, Tunnicliffe 1981). This naturally low sexual recruitment rate has been exacerbated by the decline in the abundance of the reproductive adult population (Kojis and Quinn 1993, 2001, Quinn and Kojis 2005, 2006a, 2006b).

Hughes (1994) used the term "phase shift" to describe the change from a coral dominated to an algal dominated reef community on the north coast of Jamaica near Discovery Bay. The recent rapid increase in live coral cover, particularly in the abundance of *A. cervicornis*, at Dairy Bull Reef on the north coast of Jamaica, suggested that a "phase shift reversal" from an algal dominated to a coral dominated reef community was possible (Idjadi *et al*. 2006). However, in 2005 a severe bleaching event impacted reefs on the north coast of Jamaica. This paper describes the impact of the 2005 bleaching event on the Dairy Bull Reef corals, with an emphasis on the impact on *A. cervicornis*, and compares these results to those at the nearby east Rio Bueno reef.

MATERIALS AND METHODS

Water Temperature: A Hugrun Seamon brand underwater temperature recorder with an absolute accuracy of $\pm$ 0.05 ºC was deployed at a depth of 8 m at Dairy Bull Reef (DBR) (18º28.04' N; 77º23.10' W), < 2 km from the West Fore Reef (WFR) site (18º28.17' N; 77º24.49' W), from 21 December 2000 to 15 May 2002. It recorded 11,707 hourly subsurface seawater temperature (S3T) observations. The UTR was placed adjacent to a rich coral reef community ~ 5 cm above the seabed to allow for a good flow around the recorder. The recorder was moved to the WFR (depth: 11 m) and recorded 27,735 hourly S3T observations from 2 November 2002 to 31 December 2005. The sites were considered similar and the data pooled. Gaps in both data sets were the result of equipment failure.

Coral Recruitment: Coral recruitment arrays were constructed by attaching four 208 cm^2 unglazed terracotta tiles to a PVC array. The tiles were smooth on one side and had 12 ridges on the other side. Two tiles were oriented horizontally and two vertically on each array. Paired arrays were installed at DBR at 9 m depth with the tiles ~ 0.8 m above the substrate in early April 2003. They were replaced eight months later in December 2003 ("summer 2003" sampling period), ten months later in late October 2004 ("winter / summer 2004"), nine months later in July 2005 ("winter 2005") and finally collected four months later in November 2005 ("summer 2005"). After removal from the site, the tiles were fixed in formalin and bleached. Scleractinian corals were counted (standardized to number recruits m^{-2}) and identified to family where possible using a binocular microscope.

Coral Surveys and Bleaching: Structured quantitative surveys were conducted between September 2005 and June 2006 along 20 m transect lines parallel to the depth contours at the 7 - 10 m depth range at DBR (n=10) and at East Rio Bueno (ERB) (n=8) (18º28.47' N; 77º 25.50'W). The structured quantitative surveys consisted of recording data at 0.5 m intervals under the transect line in accordance with standard Reef Check protocol (Hodgson and Liebeler 2002). Additionally, when corals were encountered, the species was identified and the following attributes recorded: presence or absence of bleaching, percent of colony bleached, and evidence of recent presence of predators. If the coral was recently killed, this was recorded this as well. The percentage of coral colonies bleached and the average percentage of bleaching 1 m on each side of each transect line was estimated. Qualitative assessment of overall bleaching was carried out from September 2005 to June 2006 during 60-75 min dives (n=25) by estimating the percentage of colonies bleached at depths 2-35 m. Photos representative of the coral community at each survey location were taken both along the Reef Check transects and during the random surveys and subsequently used in the analysis. From the photos the percent bleaching of the dominant coral present in each photo was estimated. Based on all three data sets, the extent of bleaching was determined.

RESULTS

Water temperature: The daily subsurface seawater temperature (S3T) was higher from mid May to mid October 2005 than for this period in each of the years 2001-2004 (Fig. 1). The mean monthly S3T from April to November 2005 was above the mean monthly temperature for April to November 2001-2004 (Fig. 2). Mean monthly S3T in 2005 remained at least 0.69°C warmer than the mean for the previous four years from April through October (Table 1) with the greatest difference between the mean monthly S3T in May (1.05°C) and September (0.88°C). The warmest S3T recorded during the five years of this study was 30.45°C, which occurred at 17:00hr on 29 September 2005, a couple of weeks after the initial observation of the onset of bleaching. The period mid May to mid October was characterized by calm seas and clear to partly cloudy days (pers. obs.).

Coral Recruitment: Spat from the family Poritidae were the most common (39.7%) at Dairy Bull Reef (DBR) followed by unidentifiable spat (25.2%), Agariciidae (23.2%), Milleporidae (11.3%) and Acroporidae (0.7%). Of the 302 Scleractinia and *Millepora* spat recorded on settlement plates at DBR, two acroporid recruits were observed, only one of which was large enough to identify to species. The identifiable recruit was an *Acropora cervicornis* 8.5 cm in length. It recruited to a tile that was deployed for 8.5 months (from 25 Oct 04 to 11 July 05), exhibiting an annualized growth rate of at least 12 cm year^{-1}.

Coral Bleaching: At the beginning of 2005, the scleractinian live coral cover at DBR was high, creating a structurally complex and visually appealing reef. Of the 56% total live coral cover, 44% was *A. cervicornis*. In early September 2005, the onset of bleaching was first observed in colonies of the *Montastraea annularis* complex when portions of colonies began to pale or turn white (Fig. 3). By mid September all species of scleractinan coral at DBR (except *Dendrogrya cylindrus*) showed some signs of bleaching.

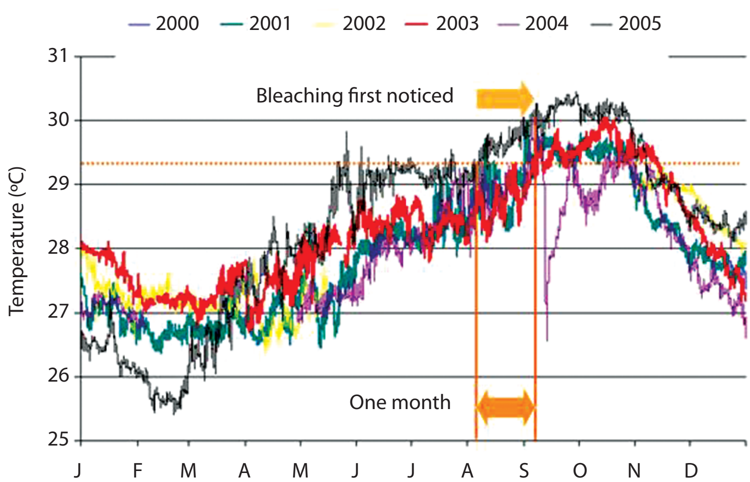

Fig. 1. Mean monthly subsurface sea water temperatures 21 December 2000 – 31 December 2005 (modified from Quinn and Kojis 2003a).

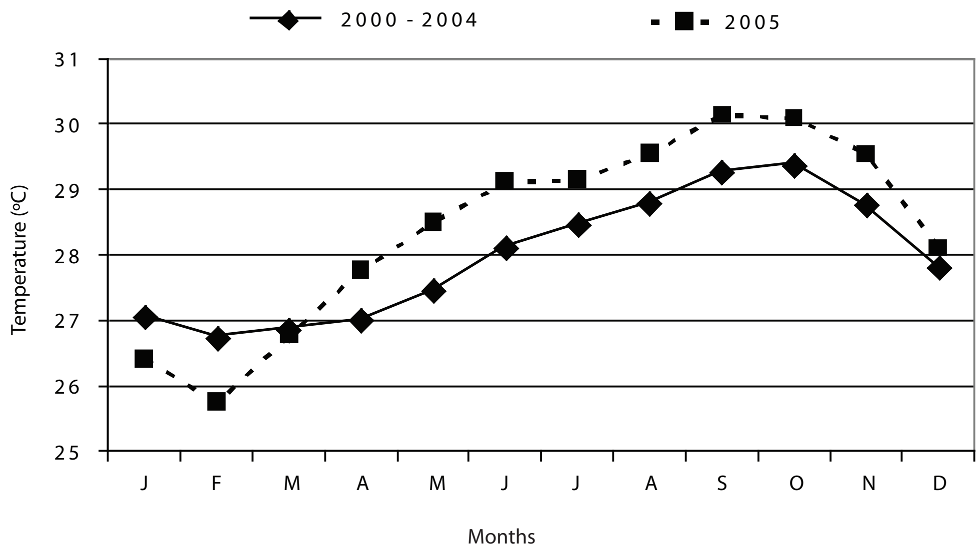

Fig. 2. Comparison of 2005 mean monthly subsurface sea water temperature with mean temperatures from 21 December 2000 - 31 December 2004.

Fig. 3. *Montastrea annularis* at initial stages of bleaching in September 2005 at 9 m at Dairy Bull Reef.

TABLE 1

Mean monthly sea water temperatures in °C: Years 2001-2004 versus 2005

Year	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	mean
2001-04	27.06	26.74	26.86	27.00	27.45	28.11	28.46	28.78	29.27	29.38	28.76	27.85	27.98
2005	26.42	25.76	26.78	27.77	28.50	29.12	29.15	29.55	30.14	30.09	29.54	28.11	28.41
Difference °C	-0.64	-0.98	-0.08	0.76	1.05	1.01	0.69	0.76	0.88	0.71	0.78	0.26	0.43

From October to December 2005, the percentage and degree of colonies bleached of each species varied widely (Table 2a, 2b). However, more than 50% of colonies of most species bleached at DBR and ERB with more than 95% of colonies of *A. cervicornis*, *Agaricia* spp., *Leptoseris cucullata*, *Meandrina meandrites, M. annularis, Porites* spp.*, Siderastrea siderea* and *Acropora* spp. bleaching. Only *A. cervicornis* exhibited 100% bleaching at both sites with100% of colonies bleached totally white (Table 2a, b).

Mortality varied widely between species and sites. In late December 2005 / January 2006, the highest mortality from bleaching was exhibited by *A. cervicornis* at DBR with 90% mortality (Table 2a). In contrast, *A. cervicornis* at ERB reef exhibited only 10% mortality (Table 2b). *A. palmata* colonies at West Rio Bueno recovered from the bleaching, but were observed being preyed upon by the coral snail, *Coralliophila abbreviata*, in February 2006. Mortality was readily noted because filamentous algae were beginning to cover the skeletons of recently killed coral.

In February, 2006, surviving remnants of *A. cervicornis* at DBR were observed to be preyed upon by the *Coralliophila abbreviata*. There was also evidence of predation by the bearded fire worm (*Hermodice carunculata*). Predation on *A. cervicornis* by these two species was not observed at ERB.

From February to June 2006, the remaining live tissue on surviving bleached colonies, including *A. cervicornis*, began to progressively regain its natural color. However, by June 2006 at DBR, there was less than <0.5% live coral cover of *A. cervicornis* (Fig. 4).

DISCUSSION

Idjadi *et al*. (2006) described a "phase shift reversal" on Dairy Bull Reef (DBR) in which live coral cover increased to 1970 levels and macroalgal cover decreased to levels recorded prior to *Diadema* mortality of 1983-84. They declared that the benthic community at DBR in 2004 was reminiscent of the fore reef

TABLE 2A

Percentage of colonies bleached and average degree of bleaching for some common scleractinians, gorgonians and sponges observed from Sept. 2005 – Feb. 2006 at Dairy Bull Reef

Species	% of colonies bleached	Degree of bleaching	Colony mortality related to bleaching
Scleractinia			
Acropora cervicornis	100%	totally white	90%
Acropora palmata	100%	Totally white	Occasional colonies completely dead, mostly PM50
Agaricia lamarcki	95%	totally white	PM50
Agaricia agaricites	95%	totally white	PM50
Colpophyllia natans	66%	pale to totally white	PM50
Diploria strigosa	66%	pale to medium	very rare
Dendrogyra cylindrus	50%	slight paleness	none
Leptoseris cucullata	95%	totally white	PM50
Madracis decactis	60%	pale	PM50
Meandrina meandrites	95%	severe – mostly white	none
Montastraea annularis complex	99%	very pale to totally white	Some mortality in smaller colonies, mostly PM25
Montastraea cavernosa	5%	some colonies pale spots	none
Porites astreoides	100%	slight color change	none
Porites porites	99%	severe	PM50
Siderastrea siderea	95%	severe – colonies colored pale blue	PM75
Siderastrea radians	50%	severe – colonies colored pale blue	PM25
Stephanocoenia intersepta	50%	pale	none
Gorgonians			
Eunicea calculata	5%	occasionally pale	none
Plexaurella nutans	5%	occasionally pale	none
Pseudopterogorgia sp	0%	no bleaching	none
Sponges			
No evidence of bleaching	0%	no bleaching	none

Data blended from surveys described in Materials and Methods.

Legend: Partial mortality in ≤25% of the colonies, PM25; partial mortality in >25% and ≤50% of the colonies, PM50; partial mortality in >50% of the colonies, PM75.

TABLE 2B

Percentage of Acropora cervicornis *and* A. palmata *colonies bleached observed from Sept. 2005 – Feb. 2006 at Rio Bueno Reef*

Species	% of colonies bleached	Degree of bleaching	Colony mortality related to bleaching
Acropora cervicornis	100%	Totally white	10%
Acropora palmata	100%	Totally white	15%

Data blended from line transects and random photo surveys.

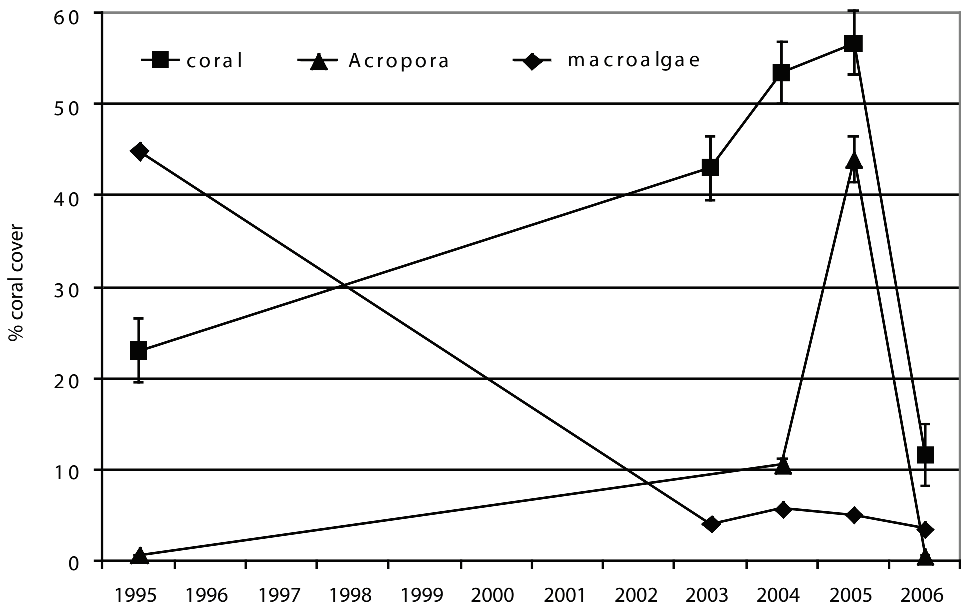

Fig. 4. Mean percentage cover of: live coral, *Acropora* spp., and macro algae at Dairy Bull Reef, in 1995, 2003, 2004 (from Idjadi *et al.* 2006), 2005 and 2006 this study. Bars represent SE.

community structure present at Discovery Bay prior to Hurricane Allen with dense thickets of *Acropora cervicornis* lodged between colonies of *Montastraea annularis* and surmised that colonies of *M. annularis* provided topographic complexity that may have facilitated the recovery of the DBR reef. The term “phase shift” was originally used to describe the overgrowth of north coast Jamaica coral reefs in 1983 by algae associated with the mass die off or the sea urchin, *Diadema antillarum* (Hughes 1994). Other work on long term changes of coral reefs all around Jamaica concluded that the sites that Hughes studied gradually became eutrophic in the early 1980s, while coral reefs on other parts of Jamaica also transitioned from coral to algal dominated reefs between the 1950s to the 1990s depending on the increase of the local human population and influx of sewage effluents (Goreau 1992).

In 2005, the reefs on the north coast of Jamaica near Discovery Bay were heavily impacted by a bleaching event. The summer of 2005 was unusual in that there were extensive periods of low wind velocity, clear skies, calm seas and low turbidity. These conditions favored localized warming and high penetration of ultra violet radiation (UVR). It is most likely that the prolonged, unusually warm seawater temperature, exceeding ≥29.3°C for one month, the predicted threshold for inducing bleaching (Goreau *et al*. 1993), was the major cause of the 2005 bleaching event. In 2005, 29.3°C was first recorded on May 22, which was the earliest that this temperature had been observed in the period 2001 – 2005 (Fig. 1) (Quinn and Kojis 2003a). Although the temperature remained above 29°C during June and July, a month of consecutive daily temperatures exceeding 29.3°C did not accrue until September 7. Coral bleaching was first observed on a dive conducted on the same date.

After the bleaching event of 2005, live coral cover at DBR decreased dramatically to well below the pre "phase shift reversal" levels recorded by Idjadi *et al*. (2006). Total live coral cover declined from 56% in 2005 to 11% in 2006. In fact, the 2006 level was 12% less than the 23% cover recorded in 1995 by Idjadi *et al*. (2006).

Acropora cervicornis was a major contributor to the increase in live coral cover reported by Idjadi *et al.* (2006) at DBR, comprising nearly 20% of the total live coral cover. In 2005 (this study), total live coral cover was similar to 2004, while *A. cervicornis* now comprised >75% of the live coral cover. Although, the different survey methodology used in this study may have contributed to the >50% increase in *A. cervicornis* abundance recorded in 2005 (Fig. 4), there are other factors that may have contributed to the decline in the contribution of other coral species to total live coral cover and the rapid increase in *A. cervicornis*. During 2003-2004, black band disease infected many *M. annularis* colonies and killed large sections of many colonies (Quinn, personal obs.). This event was overshadowed by the massive increase in *A. cervicornis* at DBR. With its high growth rate and branching structure *A. cervicornis* was able to rapidly cover large areas of the reef obscuring smaller species during transect surveys and giving the impression of a dynamic, healthy reef while masking the decline in the *M. annularis* population.

Surveys conducted in late June 2006 revealed that <0.5% of the *A. cervicornis* population at DBR was still alive. The high mortality of *A. cervicornis* from the 2005 bleaching event and subsequent predation of the scattered remnants of live tissue by *Coralliophila* and *Hermodice* explains most of the decline in live coral cover at DBR, since *A. cervicornis* provided the majority of live coral cover.

In contrast, the population of *A. cervicornis* at East Rio Bueno (ERB) had much less mortality. Live coral cover declined only 8%, from 47% in April 2004 to 39% in January 2006. The intermittent high levels of turbid water from the Rio Bueno River may have protected the colonies at ERB from UV radiation, which possibly worked synergistically with temperature to cause bleaching of corals in clear water (Jokiel 1980, Gleason and Wellington 1993). As well, the cooler river water may have helped to moderate an increase in S3T at this site. Bleaching could also have been mitigated by the high algal cover at this site. Algal cover dominated by a Rhodophyta assemblage at ERB was high in 2005 and remained high in 2006.

While the 2005 bleaching event around DBR was extensive, it was unlike the events occurring on the bleached reefs of the U.S. Virgin Islands as no outbreak of disease (Miller *et al*. 2006) or overgrowth of the encrusting tunicate *Trididemnum solidum* were observed (pers. obs.). Also, at the Jamaican study sites total mortality was low for many coral species (Table 2a, b).

This study documents a very different interpretation of the factors influencing the "phase shift" changes. Elevated subsurface sea water temperatures apparently alter the population structure and diversity of a coral reef much fast than eutrophication, over fishing and herbivore mortality. As well, the recovery of DBR will likely be inhibited by the severe impact of bleaching on key species associated with the "phase shift reversal" described by Idjadi *et al*. (2006). Because *A. cervicornis* reproductive strategy emphasizes asexual fragmentation over sexual recruitment (Tunnicliffe 1981) and the remaining populations are so small and subject to intense predation, it is considered unlikely that acroporids will rapidly recover at DBR. A site inside Discovery Bay with a formerly large population of *A. cervicornis* has not recovered in almost three decades (Wapnick *et al.* 2004).

The reasons for the lack of recovery of the acroporids on the north coast of Jamaica are myriad but doubtlessly include the severe reduction in gamete producing adults (Quinn and Kojis 2006a) and the low survival of fragments due to predation. During a 49 month period only seven acroporid spat recruited to terracotta tiles deployed at 3m and 9m on the WFR (Quinn and Kojis 2006b) and during 32 months only a two acroporid spat recruited at DBR. Acroporid settlement represented 0.7% of the total coral settlement during the entire sampling period. In contrast, recruits of Poritidae and Agariciidae were abundant on settlement plates and these two species can be expected to rebound fairly quickly after a bleaching event at the Jamaican sites, if a sufficient number of colonies survive.

Acroporidae spat settlement rates in the Caribbean are commonly lower than other coral families (Rylaarsdam 1983) in the region and much lower than Acroporidae settlement rates on reefs in the South Pacific (Kojis and Quinn 2001, Quinn and Kojis 1999, 2003b). Current observations suggest that the long-term survival of *A. cervicornis* is threatened by a number of factors including bleaching, disease, predation, and a low rate of sexual recruitment (Knowlton *et. al*. 1981, Woodley *et al.* 1981). Given the overall severe decline and local extinction of populations of *A. cervicornis*, it is unlikely that this species will recover unless successful recruitment of sexually produced planulae occurs.

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RESUMEN

La estructura de la comunidad de la mayoría de los arrecifes del Caribe ha cambiado dramáticamente desde la década de 1980. Invocando una analogía de la química, Hughes llamó en 1994 a este fenómeno un "cambio de fase" para describir el cambio de un hábitat dominado por corales a uno dominado por macroalgas en la costa del norte de Jamaica. La pérdida de cobertura coralina es ejemplificada por la muerte de *Acropora* spp. en Discovery Bay, Jamaica. Antes de 1970, eran características de las comunidades coralinas de profundidades bajas e intermedias caribeñas, las acumulaciones densas, altas y monoespecíficas de *Acropora palmata* (coral cuerno de alce) y de *A. cervicornis* (coral cuerno de venado). A inicios de la década de 1980, la cubierta coralina viva de *A. cervicornis* era >21% en varios sitios alrededor de Discovery Bay, pero para 1987 había declinado a menos de 1%. No se reestablecieron poblaciones grandes de *Acropora* en la vecindad del Discovery Bay por casi dos décadas. En 1995, la cubierta de *A. cervicornis* en Dairy Bull Reef (DBR) era de 0.6% y aumentó a cerca de 10.5% en 2004. Para 2005, la cobertura de *A. cervicornis* aumentó hasta 44%. Este aumento en la cobertura de *A. cervicornis* es parte de una importante "reversión de fase" informado por Idjadi *et al.* en 2006. Una población aislada de *A. cervicornis* exhibió una cobertura coralina similar en Río Bueno (ERB). En 2005, ambas poblaciones del *A. cervicornis* se blanquearon. Sin embargo, las dos poblaciones respondieron de manera diferente. El blanqueamiento diezmó la población de *A. cervicornis* en DBR; los sobrevivientes fueron atacados por *Coralliophilia*, y la cobertura *A. cervicornis* habia declinado a <0.5% en junio 2006. La población en ERB se recuperó del blanqueamiento con una disminución mínima en la cobertura de coral. El reclutamiento coralino fue examinado durante tres períodos de reproducción en DBR. Solamente hallamos dos reclutas de *Acropora* en los azulejos - uno en 2003 y otro en 2005. Los *Acropora* representaron solamente el 0.7% del total de reclutas en los azulejos durante todo el período de muestreo.

Palabras claves: *Acropora cervicornis*, restauración, reclutamiento, plánula.

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