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Catastrophic Loss of *Acropora palmata* in the Florida Keys: Failure of the 'Sorcerer's Apprentice Effect' to Aid Recovery Following the 2005 Atlantic Hurricane Season

James W. Porter[1], Meredith K. Meyers[1], Rob Ruzicka[2], Michael Callahan[3], Michael Colella[2], James Kidney[2], Steve Rathbun[4], and Kathryn P. Sutherland[5]

[1] Odum School of Ecology, University of Georgia, Athens, GA 30602, USA
[2] Florida Fish and Wildlife Research Institute, St. Petersburg, FL 33701, USA
[3] Department of Marine Sciences, University of South Florida, St. Petersburg, FL 33701, USA
[4] School of Public Health, University of Georgia, Athens, GA 30602, USA
[5] Department of Biology, Rollins College, Winter Park, FL 32789, USA
Corresponding author: jporter@uga.edu

Abstract. Climate change scenarios predict stronger and more frequent hurricanes. We studied survival patterns of *Acropora palmata* during the hyper-active 2005 Atlantic Hurricane Season [AHS] to assess future effects of routinely elevated storm seasons. Before the start of the 2005 AHS, 105 colonies on three survey reefs in the EPA/NOAA Coral Reef Monitoring Project were marked and tracked through 2007. Only 13 of the original 105 marked colonies survived the 2005 AHS (12%). When grouped into classes based on a combination of size, morphology, and position, results show a highly significant interaction between these classes and survivorship (*Chi Sq.* = 23.61; d.f. = 1; $\rho < 0.0001$). None of the large, 3-D exposed corals, and few of the medium, 3-D exposed corals survived. By contrast, highest survivorship occurred among small, 2-D protected corals. Medium-sized, 2-D protected corals had intermediate survival rates. None of the corals that were loose on the bottom survived. By asexual reproduction mechanisms such as breakage and fission, the so-called 'Sorcerer's Apprentice Effects,' these 13 original colonies were represented on the post-hurricane reef by 33 distinct propagules (9 pieces by breakage and 24 by fission). None of the colonies formed by breakage and only 3 of the colonies formed by fission remained by 2007. No putative sexual recruitment was observed in the two years following the 2005 AHS. As a matter of public policy, we should undertake colony cementation and snail removal as perhaps the only way to promote *Acropora palmata* regrowth and recolonization following catastrophic disturbances.

Key words: Florida Keys, Hurricanes, *Acropora palmata*, Size-class distribution, 2005 Atlantic Hurricane Season.

Introduction

Population declines in elkhorn coral, *Acropora palmata* (Lamarck, 1816), have occurred throughout the Caribbean and particularly in Florida (Bruckner and Bruckner 2001; Miller *et al*. 2002a and 2002b; Patterson *et al*. 2002; Precht *et al*. 2002; Lirman 2003; Bruckner 2003; Sutherland and Ritchie 2004; Baums *et al*. 2005; Grober-Dunsmore *et al*. 2006). As documented by the Keys-wide Coral Reef Evaluation and Monitoring Project (Porter *et al*. 2002) there has been an 95% reduction in cover by this species since the CREMP inception in 1995 (Sutherland and Ritchie 2004 Somerfield 2008).

Hurricanes exert a major control over population size in elkhorn coral both in Florida (Ball *et al*. 1967; Miller *et al*. 2002a; Lirman 2000a and 2000b; Lirman 2003; Gardner *et al*. 2003 and 2005; Garrison and Ward 2008; and Williams *et al*. 2008) and throughout the Caribbean (Bythell *et al*. 2000; Dizon and Yap 2006; Macintyre *et al*. 2007; Crabbe *et al*. 2008).

The 2005 Atlantic Hurricane Season was the most active in recorded history (National Climatic Data Center 2006). There were a record-setting 27 named storms. Fifteen of these storms became hurricanes, surpassing the 1969 record of 12 hurricanes. Seven were classified as major hurricanes ($\geq$ Class 3), and,

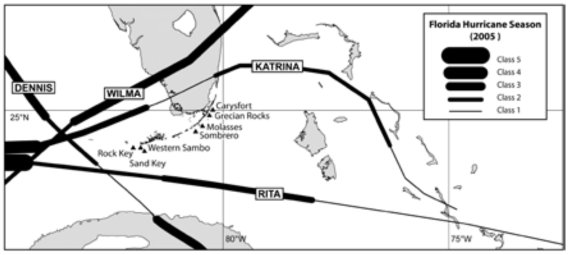

Figure 1: With 27 named storms, the 2005 Atlantic Hurricane Season was the most active on record. The map shows storm tracks and storm intensity for the four hurricanes (Dennis, Katrina, Rita, and Wilma) that influenced coral survival in south Florida during 2005. Fate tracking of *Acropora palmata* colonies occurred at shallow-water coral reefs on Grecian Rocks in the Upper Keys, and on Western Sambo and Rock Key in the Lower Keys. Long-term monitoring of *A. palmata* colonies also occurred at Carysfort, Molasses, Sombrero, and Sand Key reefs.

of these, an unprecedented number (4) reached Category 5 status. Starting in July, 2005, and continuing with a high degree of regularity over the next four months, 4 hurricanes entered the territorial waters of, or made landfall in, the State of Florida, in order of their appearance: Hurricane Dennis (July 4) ; Hurricane Katrina (August 23); Hurricane Rita (September 18); and Hurricane Wilma (October 17) (Fig. 1). These storms generated sustained winds over the reef tract of 22 – 33 m s^{-1} (43-64 knots).

This paper quantifies patterns of *Acropora palmata* loss during the 2005 Atlantic Hurricane Season by examining the influence of size, morphology, and growth position on colony survivorship. We present data on patterns of recruitment failure in the two years following the 2005 Hurricane Season. Finally we make specific recommendations to promote elkhorn coral survival in the Florida Keys.

Materials and Methods

Survey Methods

In 2005 we used fixed survey pins as reference points (Porter *et al*. 2002) to mark the positions of 105 elkhorn colonies on three of these reefs (Fig. 1). The three reefs investigated included: (1) Grecian Rocks (GR) in the Upper Keys (25^o 06.450' N. Lat.; 80^o 18.410' W. Lon.; 2.5 – 3.5 m depth), (2) Western Sambo (WS) in the Lower Keys (24^o 28.7708' N. Lat.; 81^o 43.0293' W. Lon.; 2.5 – 4.0 m depth), and (3) Rock Key (RK) in the Lower Keys (24^o 27.2893 N. Lat.; 81^o 51.4406 W. Lon.; 2.0 – 3.0 m depth). All elkhorn coral colonies within 10 m of two fixed stakes on each reef were identified by recording the distance (± 1 cm) and bearing (± 2^o) between the fixed survey pin and the target coral colony.

Elkhorn coral colonies were classified *a priori* into three categories. These categories included three classes of colony size [small (< 5 cm), medium (5 – 10 cm), and large (10 – 50 cm)]; two classes of colony morphology [2-D (encrusting) or 3-D (branching)]; and three classes of colony position [(a) exposed (upright in the water column), (b) protected (sheltered in a depression), or (c) loose on the bottom]. To determine if a colony were either "exposed" or "sheltered," a 3-4-5 right-angle triangle was constructed under water using 6', 8', and 10' PVC pipe sections. With the 30^o point of the triangle placed directly above the center of the elkhorn colony, the apparatus was rotated slowly 360^o around the colony. If the colony could be seen by viewing at a 60^o angle down the long side (10') of the triangle, then the colony's growth position was defined as "exposed." If the colony could not be seen, then its growth position was listed as "protected."

Statistical Methods

The data are comprised of a cross tabulation of morphology, size, position and survivorship at each of three sites within the Florida Keys. Analyses examined two-way contingency interactions between survivorship and each of the three factors: morphology, size and position. To adjust for variation among sites, a generalized Cochran-Mantel-Haenzel test (Agresti 1990) was used to assay for independence between survivorship and each of the three factors (Venzon and Moolgavkar 1988).

Results

All of the loss documented between 2005 and 2006 was visibly due to hurricane damage and not to

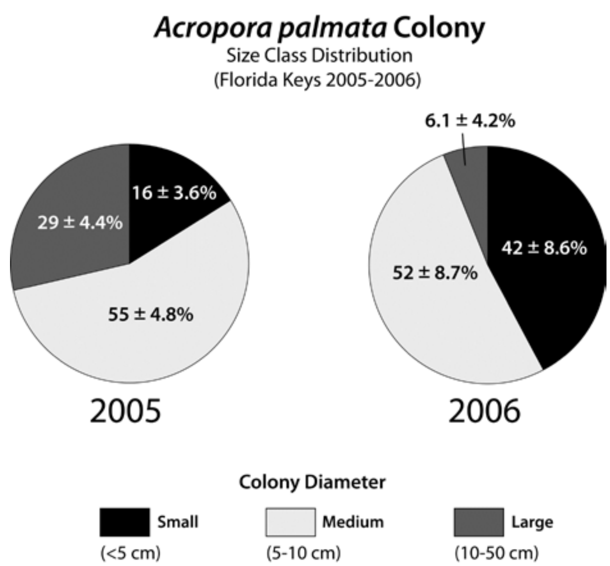

Figure 2: The pre- and post-hurricane size class distribution of *Acropora palmata* colonies in the Florida Keys shifted from larger adult colonies (left) to smaller juvenile colonies (right) as a result of the 2005 Atlantic Hurricane Season. Corals in the smallest size class (< 5 cm in diameter) increased their proportion of the population from 2005 to 2006; by contrast, large colonies (10 – 50 cm in diameter) lost proportional representation.

bleaching. It was, however, not always possible to attribute colony damage to a specific storm event.

Only 13 of the original 105 marked colonies (12%) survived the 2005 Atlantic Hurricane Season. But by asexual reproduction mechanisms such as breakage and fission, 'Sorcerer's Apprentice Effects,' these 13 original colonies were represented on the post-hurricane reef by 33 distinct propagules (9 pieces by breakage, and 24 by fission). However, none of the colonies formed by breakage and only 3 of the colonies formed by fission remained by 2007.

The data show that the greatest impact of the hurricanes was on WS, followed by RK and GR. The relative magnitude of survival rates, based on the two largest colony sizes, is GR > RK > WS. Reefs in the Upper Keys were hit less often and with weaker storms than reefs in the Lower Keys (Fig. 1). Due to small colony numbers on the post-hurricane reef, we looked for a 3-way interaction between morphology, survival, and site. The absence of this interaction (Likelihood Ratio Test, $p < 0.5$) allowed us to pool the data from all three sites.

Colony Size

Size class distribution changed significantly between 2005 and 2006 (Fig. 2). Corals in the smallest size class (< 5 cm in diameter) increased their proportion from 16.2 ± 3.6 % of the population on the pre-hurricane reef to 42.4 ± 8.6 % on the post-hurricane reef. By contrast, large colonies (10 – 50 cm in diameter) lost proportional representation, dropping from 28.6 ± 4.4 % to 6.1 ± 4.2 % % in the post-hurricane population (Fig. 2). Survival for small coral colonies (17.6 ± 5.6 %) was much greater than for large colonies (3.3 ± 3.2 %).

Colony Position

There was no statistically significant relationship between colony survivorship and colony size ($X^2_{CMH} = 2.49$; d.f. = 1; ρ = 0.11) (Table 1). However, there was a significant interaction between survivorship and colony position ($X^2_{CMH} = 13.39$; d.f. = 1; ρ = 0.0003) (Table 1), with colony survivorship highest for corals protected in a depression, and lowest for corals exposed in the water column or loose on the bottom .

Colony Morphology

There was also a significant interaction between colony survivorship and colony morphology ($X^2_{CMH} = 11.94$; d.f. = 1; ρ = 0.0005; Fig. 3; Table 1), with survivorship significantly higher in two-dimensional than in three-dimensional colonies (Fig. 3). When grouped into four classes based on a combination of size, morphology, and position, results show a highly significant interaction between these classes and survivorship ($X^2_{CMH} = 23.61$; d.f. = 1; ρ < 0.0001) (Table 1): none of the large, 3-D exposed corals, and very few of the medium, 3-D exposed corals, survived. By contrast, high survivorship occurred among small, 2-D protected corals.

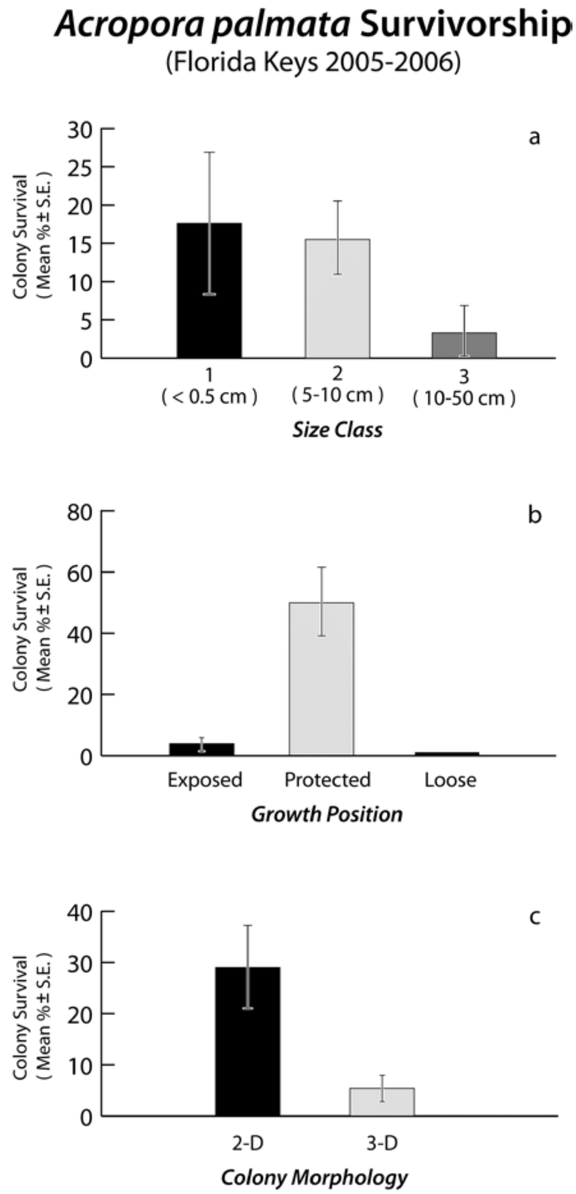

Figure 3: Survival of *Acropora palmata* colonies as a function of colony (a) size, (b) growth position, and (c) morphology. Bar graphs of the percent colony survival (mean percent ± S.E.) between 2005 and 2006 of elkhorn coral colonies demonstrate the importance of colony size (a) for small (< 5cm), medium (5 – 10 cm), and large (10 – 50 cm) colonies. Survival rates were highest for small colonies, and lowest for large colonies. Colonies growing in depressions (protected) had much higher survival rates than exposed colonies or colonies loose on the bottom (b). Skeletons with 3-D branches were more susceptible to damage or removal by hurricanes than sheeting colonies without branches (2-D) (c).

Table 1. The relationship between *Acropora palmata* survivorship and colony position, morphology, and size class.

Colony Position	**Colony Survivorship**	**Standard Error**
Exposed	0.0395	**0.0947**
Protected	0.5000	**0.1777**
Loose on the bottom	0.0000	–
Morphology		
2-D	0.2812	**0.1288**
3-D	0.0563	**0.0473**
Class		
1. Large, 3D, exposed	0.0000	–
2. Medium, 3D, exposed	0.0571	**0.0664**
3. Medium, 2D, protected	0.4545	**0.2072**
4. Small, 2D, protected	0.7500	**0.2165**

Medium-sized, 2-D protected corals had intermediate survival rates. None of the corals that were loose on the bottom in 2005 survived.

Population densities of the predatory gastropod, *Coralliophila abbreviata*, increased significantly from 0.08 / colony (± 0.33 St. Dev.; N = 105) prior to the storms (2005) to 2.77 (± 2.31 St. Dev.; N = 13) in the following year (2006), suggesting that biological predation following these catastrophic storm events contributed to the steep declines recorded in this species. Only small, well-attached colonies regrew within our study sites.

Sample size is too low for a statistically significant ordination of all combinations and permutations of size (L, M, S), morphology (2-D, 3D), and exposure (E, P, L). However, examining the four commonest combinations (1) large, 3-D, exposed, (2) medium, 3-D, exposed, (3) medium, 2-D, protected, and (4) small, 2-D, and protected colonies (Table 1) allows us to make a statistically significant ($p < 0.05$) arrangement of these from the highest to the lowest probability of survival as (4) > (3) > (2) > (1).

Discussion and Conclusions

Williams *et al.* (2008) studied five reefs in the Upper Florida Keys in the vicinity of Grecian Rocks during the same time period. Their findings are similar to those reported here for exposed colonies. In their survey, large, branching colonies decreased from 67% to 27% of the population. Our survey included reefs in the Lower Keys, which sustained more hurricane damage than Upper Keys coral reefs. Our findings show that large exposed colonies declined from 29% to 6% of the population.

It is generally believed that population regeneration in *Acropora palmata* is primarily by asexual means rather than by sexual reproduction (Highsmith *et al.* 1980; Bak and Criens 1981; Highsmith 1982; Jordan-Dahlgren 1992; Lirman and Fong 1997; Williams *et al.* 2008). There is no doubt that the branching morphology of elkhorn coral permits this type of successful recolonization following physical disturbances. Highsmith *et al.* (1980) found that high fragment survivorship following Hurricane Gerta increased the total number of colonies present and sped up recovery following the storm. This is a classic expression of the 'Sorcerer's Apprentice' effect. Lirman's hurricane model (2003) also suggests that, because sexual recruitment is limited, *Acropora palmata* can benefit from storm breakage. Under these circumstances fragmentation and regrowth may be the only mechanism available for *A. palmata* to propagate. Likewise, Fong and Lirman (1995) argue that *A. palmata* is adapted to disturbances of both low intensity and high frequency (such as occur on shallow reef-flats) as well as to episodic high intensity but low frequency events (such as hurricanes and tropical storms).

Our 2005 – 2006 data represent the outlier point for such a model. None of the 9 loose colonies observed in 2005 after the hurricanes was found alive in 2006, and all 14 broken pieces marked in 2006 were dead by 2007. Contrary to a 'Sorcerer's Apprentice' effect, what little survival occurred was exclusively by the regrowth of small, well attached colonies and not by breakage products, potentially invalidating this historically significant mechanism for reef recovery (Ball *et al.* 1967; Fong and Lirman 1995). Particularly if storm intensity, and possibly also storm frequency, increase, this reproductive strategy will have limitations in keeping *A. palmata* dominant on shallow water reef crests.

The predatory snail, *Coralliophila abbreviata*, survived the storm, with the result that snail density per coral colony increased as prey availability declined almost 90%. This suggests that biological predation following catastrophic storm events (Knowlton *et al.* 1990) will also contribute to the steep declines in this Threatened Species.

Implications for management and conservation

Post the 2005 A.H.S., elkhorn population recovery is dependent mostly on the existence of fission products and small colonies that survived the storm. Both chemical and physical aspects of water quality will be critical to this process. Ball *et al.* (1967) demonstrated the rapid recovery of *Acropora palmata* reefs after Hurricane Donna in 1965. It increasingly seems that what has changed most in the population dynamics of reef recovery is not the existence of hurricanes, but the resiliency of reefs to them. If we are entering a phase of increased storm number and intensity, then reefs are more at risk now than ever before because of their slow recovery response time.

Our data strongly support calls from researchers from the Caribbean (Bruckner and Bruckner 2001; Garrison and Ward 2008; Forrester *et al.* 2011) and

Florida (Williams and Miller 2010) who recommend cementing fragments to the reef surface as the best way to promote elkhorn survival. To muster the person-power required after natural disasters, this will inevitably mean relaxing prohibitions against touching and manipulating this Threatened Species. If the cementation efforts are guided by local coral reef conservation organizations, however, this action is likely to be the single best restoration ecology action possible.

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