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11B Phase shifts and alternative states on coral reefs

Factors contributing to the regional decline of *Montastraea annularis* (complex)

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Abstract. Over the last 15 years the massive framework coral, *Montastraea annularis* (complex) has experienced a rapid decline in abundance, size and condition, and on many reefs in the western Atlantic these species are no longer the dominant corals. Surveys conducted in Puerto Rico, the Cayman Islands, Bonaire, St. Kitts and Nevis, and the Bahamas show a similar die-off and replacement by other corals, aggressive invertebrates and macroalgae, although the timing of these events is variable. Widespread colony mortality has been triggered by mass bleaching events, with coral diseases emerging after corals began to recover from bleaching. Outbreaks of yellow band disease and white plague remain the primary threat affecting these species, although other diseases, fish predation, competition with algae, and overgrowth and bioerosion by sponges are contributing to further losses. *M. annularis* (complex) colonies have sustained the higher levels of partial and whole colony mortality than all other species. *Agaricia* spp., *Porites* spp. and other brooding species, as well as certain broadcast spawners, exhibit successful recruitment and colonization of reef substrates and exposed skeletal surfaces of *M. annularis*. In contrast, few recruits of *M. annularis* have been documented and formerly large colonies that have survived now consist of small tissue isolates that continue to shrink in size. While much attention has focused on the decline of Caribbean acroporids, the loss of *M. annularis* (complex) has more significant implications as these are much longer lived, slower growing and less able to recolonize a reef through sexual recruitment or fragmentation.

Key words: *Montastraea annularis* species complex, *M. faveolata*, *M. franksi*, coral disease, coral bleaching.

Introduction

Montastraea annularis (species complex) are the most important framework corals on western Atlantic reefs. The three species in this complex (*M. annularis, M. faveolata* and *M. franksi*) form large, long-lived corals that have been dominant for millennia (Jackson 1992). They play a critical role in reef construction and community ecology (Goreau 1959; Knowlton 1992). Until recently, they were thought to be better able to survive periods of adverse conditions than most other coral species (Johnson et al.1995).

Montastraea annularis (complex) exhibit characteristics of k-selected species, including slow growth rates, late reproductive maturity, development of large colonies with low rates of whole and partial colony mortality, and moderate regeneration capabilities (Bak and Engel 1979; Meesters et al. 1996). Colonies can be described as 'bet-hedgers' because they live for centuries, require many years before first reproduction, and exhibit some of the lowest larval recruitment rates reported for western Atlantic reef-building corals (Szmant-Froelich 1985).

The high densities of large colonies seen throughout the western Atlantic suggest that, at least until recently, these species were- less susceptible to the stressors that contributed to the demise of *Acropora* spp. and other Caribbean corals (Bythell et al. 1993). These corals are extremely robust and resistant to the effects of all but the most severe hurricanes (Woodley et al. 1981; Bythell et al. 2000). Damaged colonies also exhibit high rates of healing and survival (Bak and Engel 1979), which may be related to their large body size (Bythell et al. 1993; Meesters et al. 1996; Bak and Meesters 1998).

Since 1995, *M. annularis* (complex) have exhibited a conspicuous trend of decline due to disease, bleaching, predation, and increased competition by other benthic organisms (Bruckner and Bruckner 2003, 2006a,b; Miller et al. 2006; Edmunds and Elahi 2007; Bruckner and Hill 2009; Rogers et al. 2009). These corals are susceptible to at least 5 major diseases (Weil 2004), and they often show signs of multiple infections simultaneously (Bruckner and Bruckner 2006a). They have also been severely impacted by recent (1995, 1998, 2005, 2009) mass bleaching events. This manuscript examines the population structure of these corals within 5 countries through use of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol. Factors contributing to mortality and implications of losses are discussed.

Material and Methods

The number, size and condition of all corals, 4 cm or larger in diameter were recorded within belt transects (10 m long and 1 m wide), at three depth ranges (3-6 m, 7-12 m, and 13-18 m) off the Bahamas (Cay Sal, the Inaguas and Andros), Bonaire, the Cayman Islands (Little Cayman, Cayman Brac and Grand Cayman), Puerto Rico (Mona and Desecheo Island), and St. Kitts and Nevis (SKN) (Fig. 1). 185 sites were examined between February 2010 and October 2011.

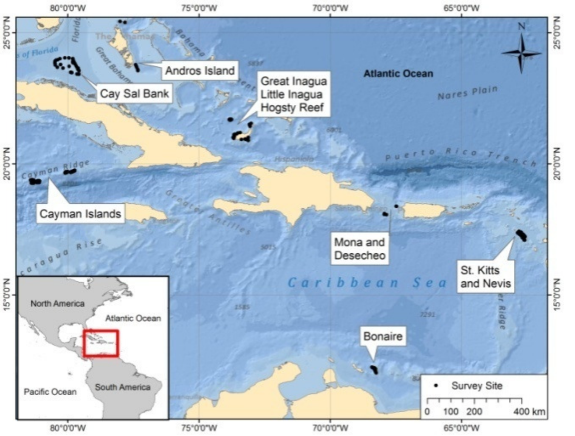

Figure 1: Location of study sites in the Bahamas, Bonaire, Cayman Islands, Puerto Rico, and St. Kitts and Nevis.

All corals within the belt transect were identified to species, measured and assessed for condition. A one meter bar, marked in 1 cm increments is used to measure the maximum diameter, width (perpendicular to the diameter), height, and amount of mortality. Mortality is categorized as: recent (occurring within the last 1-5 days), transitional (filamentous green algae and diatom colonization, 6-30 days) and old (>30 days). For each coral with recent partial or whole colony mortality, the cause of mortality was identified as a specific disease, predation, competition, overgrowth or unknown, and the extent of bleaching was recorded on a scale of 1-5. Sampling for corals smaller than 4 cm was done using a minimum of five 0.25 m^2 quadrats per transect, each located at predetermined intervals (2, 4, 6, 8, 10 m), alternating between right and left side of the transect.

Colony sizes were converted to planar surface area using the following equation: A = Pi * L/2 * W/2 and the remaining area of live tissue was determined by multiplying the original area by the percent live tissue. Statistical analysis of coral transect survey data was performed using PRIMER v6 (Clarke and Gorley 2006). Data were square root or log transformed (area) or arcsine transformed (percentages) before analysis in order to normalize data. Variation in coral composition and size structure with respect to country and species variables were tested using a 1-way Analysis of Similarity (ANOSIM). Non-metric multidimensional scaling (NMDS) was used to provide a visual summary of the Bray-Curtis similarity matrix.

Results

The three species of the *Montastraea annularis* (complex) made up 9-30% of all corals (>4 cm diameter) within belt transects, occurring at densities of 0.3-2.7 colonies/m^2 (Table 1). Abundance of *M. annularis* (complex) varied significantly among countries (Global R = 0.191, p<0.001), although abundances were not significantly different between Bonaire and the Cayman Islands (pairwise tests, R=0.028, p=0.04) or between Puerto Rico and the Bahamas (R=0.092; p=0.99) (Fig. 2). While the total abundance and cover of all other species (pooled) was greater than *M. annularis* (Table 2), and certain species (e.g. *Agaricia* and *Porites*) were numerically dominant, the total contribution to living coral cover by any individual species was substantially less than the cover of *M. annularis* (complex). Furthermore, a substantial number (18%) of colonies of other species (especially brooders) within transects had settled on the dead skeletal surfaces of *M. annularis* complex.

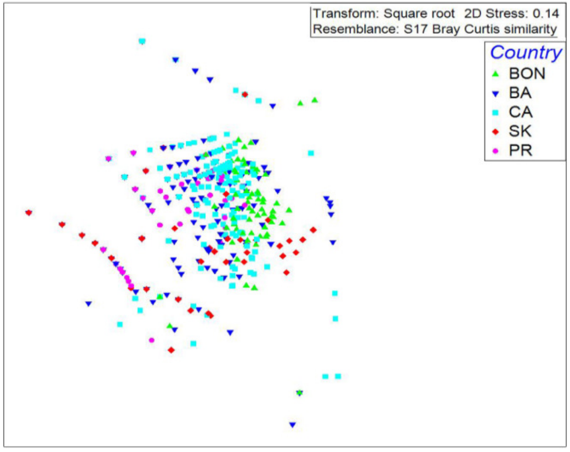

Figure 2: Nonmetric multidimensional scaling (NMDS) of M. annularis (complex) composition in Bonaire (BON), the Bahamas (BA), the Caymen Islands (CA), St Kitts and Nevis (SK) and Puerto Rico (PR). Each dot represents a 10 m belt transect.

The original skeletal surface areas of colonies of *M. annularis* (complex) were significantly larger than all other species. The mean diameter of *M. annularis* (complex) ranged from 44-89 cm (Table 1) and the size structure (planar surface area) shows a bell shaped distribution with few small colonies (<500 cm^2) and few very large colonies (>10,000 cm^2) (Fig. 3). *Montastraea faveolata* was significantly larger than *M. annularis* and *M. franksi* (ANOVA, p <0.001, F=60.06). Other species were dominated by small colonies (mean=14-23 cm diameter; Table 2) and populations exhibited a monotonic decline in size, with few colonies >60 cm diameter.

	BO	CS	AN	IN	LC	CB	GC	MO	DS	SKN
# Sites	25	31	10	32	18	12	22	6	4	25
N	1602	413	628	584	427	605	1026	627	359	922
Density	2.5	0.3	1.4	0.6	1.4	1.3	1.5	1.7	1.9	0.9
% Tot	27	9.2	30	18	25	25	25	27	27	18
Cover	23.5	0.6	3.9	3.3	6.4	6.5	5.9	7	4	2.9
Diam	53	46	38	51	44	46	45	89	70	35
Width	48	37	30	40	37	42	40	70	63	29
Height	48	36	43	51	36	41	38	54	52	27
% Old	29	43	30	50	28	26	34	65	58	39
% Rec	2.4	1.2	0.3	0.6	1.2	1.1	1.7	0.6	0.3	0.8
Mort	31.4	44.8	30.3	50.8	29.5	27.8	36.2	65.9	58.3	40.2

Table 1: Population structure and condition of *M. annularis* (complex) in Bonaire (BO), the Bahamas [Cay Sal (CS), Andros (AN), and The Inaguas (IN)], Little Cayman (LC), Cayman Brac (CB), Grand Cayman (GC), Mona Island (MO), Desecheo Island (DS) and St. Kitts and Nevis (SKN). The total number of colonies, density, % of the total coral population (%TOT, live cover, mean size (original diameter, width and height), and mean amount of partial mortality (old mortality = % Old; recent mortality = % Rec; and total mortality =Mort) are shown.

	BO	CS	AN	IN	LC	CB	GC	MO	DS	SKN
N	4352	4108	1453	2627	1276	1809	3006	1678	951	4265
Cover	25.9	6.6	5.5	6.4	16	16	19	15	12	7.7
Diam	23	14	14	15	19	20	22	36	23	15
Width	20	11	11	11	16	16	18	29	16	12
Height	17	7	8	8	13	15	15	15	14	7
Mort	8.2	8.9	9.9	16.8	9.9	8.7	10.5	16.2	9.9	8.6

Table 2: Population structure and condition of all species of corals except *M. annularis* (complex) in five countries as listed in Table 1. Total number of colonies, live cover, mean size (diameter, width and height) and mean amount of partial mortality (Mort) are shown.

Montastraea annularis (complex) exhibited higher levels of partial tissue mortality (mean= 29-66%; Table 1) than all other species (mean=8-17%). The total percent partial mortality (pooled for all sites) also varied among the three species of *M. annularis*, with significantly higher levels of tissue loss in *M. annularis* (mean=40%) and *M. faveolata* (mean = 38%) than in *M. franksi* (mean= 25%; ANOVA, p<0.001, F=75.31). Overall, the total live area occupied by these corals (the area of all corals from the five countries are pooled) declined by a mean of 38% for *M. franksi* (mean size of corals declined from 1356 cm^2 to 845 cm^2), 51% for *M. annularis* (mean size declined from 1927 cm^2 to 939 cm^2) and 65 % for *M. faveolata* (mean size declined from 4005 cm^2 to 1413 cm^2). While a number of dead colonies of *M. annularis* complex were observed (5-7% of the total), most were reduced in size but were still alive. Surviving colonies were typically divided into multiple smaller tissue remnants, with some colonies consisting of live tissue remnants of 1-3 cm diameter. These species exhibit a significant increase in small tissue remnants (0-500 cm^2; 211% for *M. annularis*, 168% for *M. faveolata,* 137% for *M. franksi*), while the proportion of large, completely live colonies (1,500- 30,000 cm^2) declined by 51-57% (Fig. 3).

A substantial decline in live tissue area was observed among all three species of *M. annularis* in the five countries (Fig. 4). However, the size structure (planar surface area) of each species and the

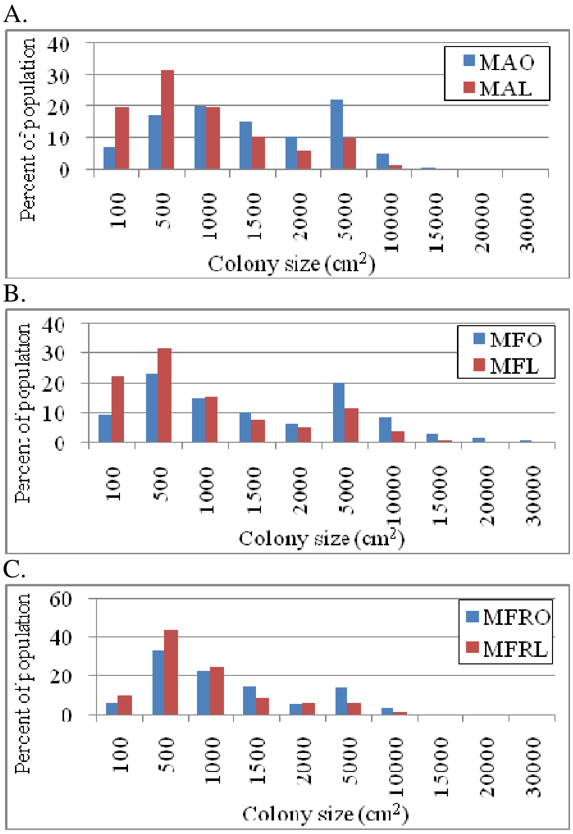

Figure 3: Original size structure (O; blue bars) and amount of remaining live tissue area in 2010/2011 (L; red bars) for A. *M. annularis*; B. *M. faveolata* (MF) and C. *M. franksi* (MFR).

amount of remaining live tissue varied between countries. In particular, *M. annularis* and *M. faveolata* colonies in Puerto Rico were much larger and these sustained higher levels of mortality. In contrast, colonies in Bonaire were also large, but these experienced much lower levels of mortality. Furthermore, an examination of the mean dead coral area for each species varied between each country (Single factor ANOVA; *M. annularis*: $p<0.001$ $F=19.473$; *M. faveolata*: $p<0.001$ $F=41.221$; *M. franksi*: $p<0.001$ $F=5.271$).

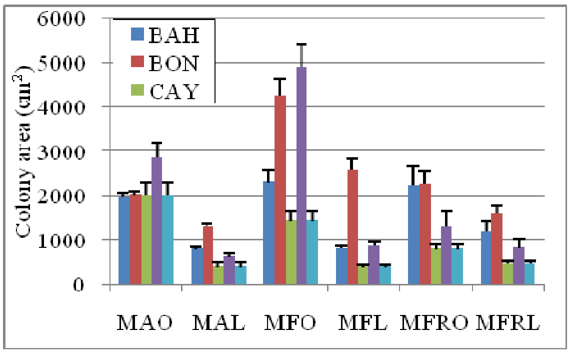

Figure 4: Mean size (planar surface area) of corals pooled by species for the five countries. Data are separated into the original (O) and remaining live tissue area (L) for *M. annularis* (MA), *M. faveolata* (MF) and *M. franksi* (MFR).

Most colonies of *M. annularis* (complex) have been divided into 2 or more smaller tissue remnants with exposed skeletal surfaces being colonized by other species of scleractinian corals, dense cover of fleshy macroalgae, bioeroding sponges and tunicates. Mortality was attributed primarily to outbreaks of coral disease (white plague and yellow band disease) which emerged as corals began recovering from mass bleaching events. this was followed by increased predation, and development of damselfish algal lawns.(Fig. 5).

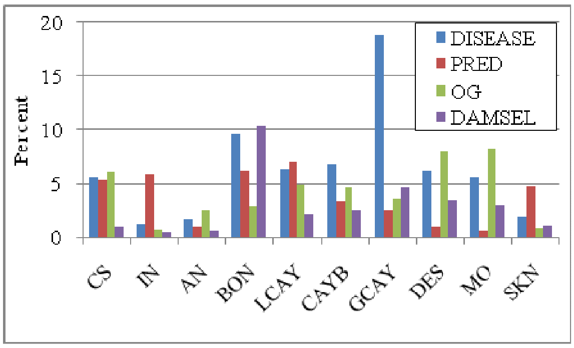

Figure 5: Prevalence of coral disease (DISEASE), snail and fish predation (PRED), overgrowth by sponges and tunicates (OG) and damselfish algal lawns (DAM) on Cay Sal (CS), Inaguas IN) and Andros (AN) Bahamas, Bonaire (BON), Cayman Brac (CB), Grand Cayman (GC), Little Cayman (LC), Mona (MO) and Desecheo (DES) Puerto Rico, and St. Kitts and Nevis (SKN).

Many locations examined showed high levels of recruits, but these are mostly *Porites, Agaricia, Siderastrea,* and 18 other species (Fig. 6). Out of 5273 quadrats in five countries, *Montastraea* recruits were identified eight times: Cay Sal (n=4), Inaguas (n=2), St. Kitts (n=1), Bonaire (n=1).

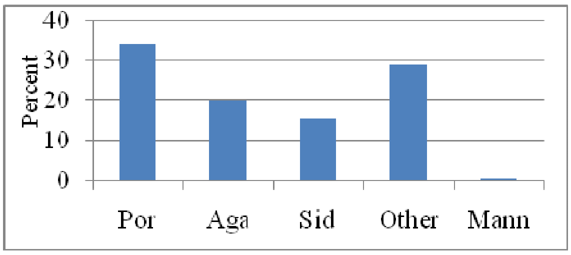

Figure 6: Recruitment within 0.25 m^2 quadrats in five countries. Por = *Porites* spp.; Aga = *Agaricia spp.*; Sid = *Siderastrea* spp.; other = 18 species; Mann= *M. annularis* (complex).

Discussion

Fore reef sites throughout the Caribbean were formerly dominated by *M. annularis* (species complex). These species exceeded other corals in abundance and cover, forming dense assemblages of large, hundreds of year old colonies and few small colonies. The historical absence of small colonies and few observed recruits, even though large numbers of gametes produced on an annual basis, suggests that recruitment events are rare, and were less important for the survival of *M. annularis* in the past, compared to short-lived brooding species such as *Agaricia* and *Porites* spp. (Hughes and Tanner 2000).

The type of tissue loss (old, transitional or recent) provides an indication of the timing and causes of mortality. In Puerto Rico, colonies experienced a slow, progress decline from yellow band disease that began after a 1995 bleaching event, with rapid loss of 30-60% of the live tissue due to a severe outbreak of white plague following bleaching in 2005 (Bruckner and Hill 2009); these diseases continued to affect remaining colonies in 2009 (this study). An outbreak of white plague was also causing extensive mortality in the Cayman Islands after colonies began recovering from a 2009 mass bleaching event. In Bonaire, outbreaks of YBD were first observed after a bleaching event in 1995, and several localized outbreaks of white plague in 2005 (Bruckner 2012) and 2010 (this study) caused extensive losses of *M. annularis* on selected reefs. In the Bahamas, mortality associated with bleaching in 1998 and 2005 appear to be important factors causing losses of these species (unpubl data). Disease prevalence was low in St. Kitts and Nevis in 2010, possibly because most *M. annularis* (complex) colonies died during or following the severe bleaching event in 2005.

The recent emergence of these extremely virulent diseases following excessive stress associated with mass bleaching events appear to be unsustainable for these taxa (Miller et al. 2006; Rogers et al. 2008), and recovery from these catastrophic and chronic events may take centuries or longer. White plague causes tissue loss at rates of cm d^{-1} or more, exceeding annual colony growth rates by 10-fold or more (Gladfelter et al. 1978; Richardson et al. 1998). YBD progresses much more slowly (1 cm mo–1), but the disease persists for prolonged periods (up to 8 yr or more), and it typically manifests in multiple locations, exacerbating the extent of tissue mortality (Bruckner and Bruckner 2006a; Bruckner and Hill 2009).

Conditions have changed regionally, and these species are disappearing from many reefs. Colonies are dying or are being reduced into small tissue remnants, yet their skeletons persist for decades, and are being colonized by other species (Bruckner 2012). In all locations examined, reefs appear to be undergoing a progressive shift in coral assemblages to a dominance by shorter lived, smaller corals.

Although, the modular life form and the ability for colonies to survive with partial mortality has been suggested to provide *Montastraea annularis* (complex) with the ability to respond rapidly to environmental and human disturbances, other competitors such as macroalgae and bioeroding clionid sponges appear to be overwhelming the remaining tissue isolates and compromising the potential for recovery of these species. Even if colonies do survive, partial tissue mortality is causing a regression of colonies to sizes that are below the threshold for successful reproduction (Szmant 1991). With predicted increases in bleaching severity and frequency, and linkages with disease outbreaks, steps must be taken to reduce manageable (human) stressors, so that surviving tissue isolates are not further compromised and are able to resheet, and grow to a larger size, and reach reproductive maturity once again.

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