Large-scale coral recruitment patterns on Mona Island, Puerto Rico: evidence of a transitional community trajectory after massive coral bleaching and mortality

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Abstract: Coral reefs have largely declined across the northeastern Caribbean following the 2005 massive bleaching event. Climate change-related sea surface warming and coral disease outbreaks of a white plague-like syndrome and of yellow band disease (YBD) have caused significant coral decline affecting massive reef building species (i.e., *Orbicella annularis* species complex) which show no apparent signs of recovery through larval sexual recruitment. We addressed coral recruit densities across three spur and groove reef locations along the western shelf of remote Mona Island, Puerto Rico: Punta Capitán (PCA), Pasa de Las Carmelitas (PLC), and Las Carmelitas-South (LCS). Data were collected during November 2012 along 93 haphazard transects across three depth zones (<5m, 5-10m, 10-15m). A total of 32 coral species (9 octocorals, 1 hydrocoral, 22 scleractinians) were documented among the recruit community. Communities had low densities and dominance by short-lived brooder species seven years after the 2005 event. Mean coral recruit density ranged from 1.2 to 10.5/m² at PCA, 6.3 to 7.2/m² at LCS, 4.5 to 9.5/m² at PLC. Differences in coral recruit community structure can be attributed to slight variation in percent macroalgal cover and composition as study sites had nearly similar benthic spatial heterogeneity. Dominance by ephemeral coral species was widespread. Recovery of largely declining massive reef-building species such as the *O. annularis* species complex was limited or non-existent. The lack of recovery could be the combined result of several mechanisms involving climate change, YBD disease, macroalgae, fishing, urchins and Mona Island's reefs limited connectivity to other reef systems. There is also for rehabilitation of fish trophic structure, with emphasis in recovering herbivore guilds and depleted populations of *D. antillarum*. Failing to recognize the importance of ecosystem-based management and resilience rehabilitation may deem remote coral reefs recovery unlikely. Rev. Biol. Trop. 62 (Suppl. 3): 49-64. Epub 2014 September 01.

Key words: Climate change, coral decline, coral recruitment, community trajectory, Mona Island, Puerto Rico, transitional state.

Coral larval recruitment is critical for the maintenance of reef biodiversity, ecosystem resilience and benthic community recovery after disturbances across multiple spatial scales (Gittings, Bright, Choi & Barnett, 1988; Sammarco, 1991; Connell, Hughes & Wallace, 1997; Hughes & Tanner, 2000). Coral recruitment refers to the stage when new members of the recently settled juvenile corals become visible to be censused (Harrison & Wallace, 1990). Open reef space is necessary for settling larvae (Hughes & Connell, 1999; Kuffner et al., 2006; Díaz-Pulido et al., 2009), particularly substrates along cryptical microhabitats and areas dominated by crustose coralline algae (CCA), which are recognized by coral larvae (Doropoulos, Ward, Díaz-Pulido, Hoegh-Guldberg & Mumby, 2012). Dynamic

processes leading to the creation of free space open for colonization are important for successful recruitment. Nonetheless, Caribbean coral reef ecosystems have shown increasing rates of large-scale disturbance, including hurricanes (Emanuel, 2005; Mann & Emanuel, 2007), massive coral bleaching events (Miller et al., 2006; 2009), widespread disease outbreaks (Cróquer & Weil, 2009; Weil & Cróquer, 2009), and the massive die off of the Long-spine urchin, *Diadema antillarum* (Phillipi 1845) (Lessios, 1988; Gardner et al., 2003), with paramount long-term impacts in adult coral assemblages and in the overall benthic community composition (Hughes, Reed & Boyle, 1987; Hughes, 1994; McClanahan & Muthiga, 1998; Rogers & Miller, 2006; Miller et al., 2009; Edmunds, 2013).

Juvenile coral depth distribution often follows the distribution of adult parental colonies (Bak & Engel, 1979; Harriott, 1985). But Caribbean-wide coral reef decline has been characterized by significant losses in percent live tissue cover of parental colonies followed up by declining trends in coral recruitment (Connell, 1997). There is mounting evidence that recent sea surface warming trends across the Caribbean associated with climate change resulted in significant shifts in coral reef benthic community structure due to the long-term impacts of the 2005 widespread massive coral bleaching that impacted at least 65% of the corals at Mona Island, including 94% of the colonies of the of Star coral *Orbicella (=Montastraea) annularis* species complex (Ellis & Solander, 1786) (García-Sais et al., 2008). This event was followed by the 2005-2006 large-scale coral disease outbreak and mortality (Miller et al., 2009; Edmunds, 2013). Diseases such as yellow band disease (YBD) significantly compromised the reproductive output of *O. faveolata* (Ellis & Solander, 1786) (Weil, Cróquer & Urreiztieta, 2009), and caused a rapid decline within the *O. annularis* species complex in Mona Island (Bruckner & Bruckner, 2006; Bruckner & Hill, 2009). These factors led to massive coral recruitment failure of multiple species, resulting in a major

decline in the natural recovery ability of critical reef-building species such as *O. annularis* (Edmunds & Elahi, 2007; Hernández-Pacheco, Hernández-Delgado, & Sabat, 2011). This has further resulted in an irreversible alteration in the trajectory of coral reef benthic community structure across very large spatial scales.

Successful coral recruitment is critical for sustaining slow-growing, low-recruiting massive coral species (Harrison & Wallace, 1990; Szmant, 1991). But several long-term studies have shown very limited sexual recruitment success for the *O. annularis* species complex (Rogers et al., 1984; Edmunds & Elahi, 2007; Irizarry-Soto & Weil, 2009), even at Mona Island (Bruckner & Hill, 2009). Edmunds (2004) also found a positive correlation between juvenile coral density and mean sea surface temperature (SST), with slower growth and higher mortality under high SST, in a pattern leading to changes in relative generic abundance. These findings suggest that even such long-term subtle effects could result in major transitional changes in benthic community composition and trajectory, with far-reaching ecological consequences for the survival and resilience of coral reefs. Further, disturbance history over multiple spatio-temporal scales is also a critical determinant of coral reef community trajectory. Hurricanes, in combination with massive coral bleaching events, have resulted in high mortality of juvenile corals (Harriott, 1985) and declining coral recruitment rates across large spatial scales (Mumby, 1999; Mallela & Crabbe, 2009). This could be the result of indirect impacts on recruitment habitat quality which may alter larval selection. Coral larvae have been shown to be highly selective of habitat conditions for successful recruitment (Baird, Babcock & Mundy, 2003; Kuffner et al., 2006). Elevated SST has been shown to alter microbial biofilm community structure associated to CCA, therefore, altering natural cues for coral larval recruitment (Webster, Soo, Cobb & Negri, 2011). Doropoulos et al. (2012) suggested that ocean acidification (OA) may also reduce coral population recovery by reducing coral larval settlement rates, disrupting

larval settlement behavior, and reducing the availability of the most desirable coralline algal species for successful coral recruitment.

Climate change has become one of the most significant and imminent threats to coral reefs at a global scale (Hoegh-Guldberg, 1999; Buddemeier et al., 2008). Recent modeling efforts have suggested that current trends in sea surface warming, increasing atmospheric CO_2 concentration, and OA might have paramount negative consequences on coral reef ecosystems and their services (Buddemeier et al., 2008; 2010), as well as in the overall marine productivity (Hoegh-Guldberg et al., 2007; Veron et al., 2009). According to McWilliams et al. (2005), a rise in regional SST of 0.1˚C resulted in up to 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively. Maximum bleaching extent and intensity are predicted to occur at regional SST anomalies of less than +1˚C (Hoegh-Guldberg, 1999). Coral bleaching is therefore likely to become a chronic source of stress for Caribbean reefs in the near future, with a high potential for coral reef decline, and significantly compromising the natural recovery ability of coralline communities and ecosystem resilience, including remote islands located far from known pollution centers.

Even remote coral reefs have undergone significant recent decline as a result of regional climate change-related impacts (Goreau, Hayes & McClanahan, 2000; McClanahan & Muthiga. 1998; McClanahan, 2000; Walther et al., 2002) and have showed limited recovery ability (Gardner et al., 2005; Sandin et al., 2008; Birkeland et al., 2013). Coral reef recovery on remote habitats depends on the functional redundancy of impacted coral assemblages, on the tissue regeneration ability and regrowth of surviving remnant colonies, and on successful coral recruitment (Golbuu et al., 2007; Díaz-Pulido et al., 2009). Genetic connectivity also plays a critical role in natural coral reef recovery (Zubillaga, Márquez, Cróquer & Bastidas, 2008). But populations for many important coral species, particularly across the Caribbean, show high genetic structuring

implying that long-distance larval dispersal is an unusual event (Baums et al., 2005; 2006; Vollmer & Palumbi, 2007; García-Reyes & Schizas, 2010; Mège, Schizas, García-Reyes & Hrbek, 2014), rendering isolated coral reefs to largely rely on remnant colony regrowth, colony fragmentation, and self-recruitment for their natural recovery from disturbance. Nonetheless, there is still scarce information regarding remote coral reef natural recovery rates and the trajectory followed by benthic communities impacted from disturbance. This study was aimed at conducting a large scale survey of coral recruit densities on the western shelf of remote Mona Island, Puerto Rico, to build on earlier reports by Bruckner and Hill (2009), and address the coral community trajectory following the 2005-2006 massive coral bleaching and mass mortality event.

MATERIALS AND METHODS

Study sites: This study was carried out in November 2012 across three spur and groove fringing reef locations along the western shelf of Mona Island, Puerto Rico: Punta Capitán (PCA, 18°06.283'N, 67°56.137'W), Pasa de Las Carmelitas (PLC, 18°06.162'N, 67°56.229'W), and Las Carmelitas-South (LCS, 18°05.995'N, 67°56.290'W). Mona is an oceanic island located 79 km off the western coast of Puerto Rico. Its origin was during the Miocene to Pliocene (10 to 4 Ma) (Rodríguez, 2012) and was suggested by González et al. (1992, 1997) to be the first extensive barrier reef complex reported in the Caribbean.

Coral recruit density: Data was collected along 93 haphazard transects (PCA n=27, PLC n=35, LCS n=31) across three depth zones (<5m, 5-10m, 10-15m). Sampling sites were randomly selected to represent replicate reef habitats along similar depth gradients and similar open substrate space available for recruitment. A maximum of 6-12 transects were analyzed per depth zone at each site. Replicate 10 m-long line transects were haphazardly established along depth contours, often parallel

to reef spurs orientation, and separated by at least 10m. Data were collected using high-resolution digital photography along 5 replicate, non-overlapping quadrats per transect (N=465 quadrats) at haphazardly fixed intervals (1, 3, 5, 7, 9m) following a slight modification from the AGGRA method (Lang, 2002), and at a fixed distance from the bottom using a 40 x 27cm (0.108m²) photoquadrat fixed to the camera housing. Any coral colony <5cm was treated as a coral recruit. Coral species with sexually mature small sizes, such as *Siderastrea radians* (Pallas, 1766), were also included in the counts as they were largely abundant across study sites. Efforts were made to avoid sampling areas with high sediment bedload and efforts were made to remove sediments from the bottom when looking from recruits. No special efforts were made to remove algae to test for percent algal cover spatial effects. Percent macroalgal cover was visually estimated from each image following AGGRA methodology (Lang, 2002).

Statistical analyses: A two-way multivariate analysis of similarity (ANOSIM) was used to test the null hypothesis of no significant difference in coral recruit density, biodiversity parameters, including species diversity index (H'n, Shannon & Weaver, 1948), and evenness (J'n, Pielou 1966), and community structure among sites and among depth zones using PRIMER-e v.6.1.14 (Clarke & Warwick, 2001). Principal component ordination (PCO) was used to determine which benthic taxa abundance explained spatial clustering patterns of coral recruit communities (Anderson et al., 2008). PRIMER's RELATE multivariate correlation routine was used to test the relationship between coral recruit abundance and percent macroalgal cover. Proportional data on coral recruit abundance and percent macroalgal cover were √-transformed prior to analysis. All tests were based in 10 000 permutations.

RESULTS

A total of 347 coral recruit colonies of 32 coral species (9 octocorals, 1 hydrocoral, 22 scleractinians) was documented, with 99 colonies at PCA, 113 at LCS, and 135 at PLC (Table 1). This included 17 species at PCA subdivided in 3 species across the shallow reef segment, 11 species across the middle depth segment, and 13 across the deeper segment. There were also 15 species at LCS subdivided in 8 species across shallow, 7 across the middle, and 10 across the deeper segment. A total of 18 species of coral recruits were observed at PLC, with 9 species across the shallow, 8 across the middle, and 16 across the deeper zone. Coral recruit community structure was significantly different among locations (*p*=0.0260), particularly between PCA and LCS (*p*=0.0060), but not among depth zones (Table 2). There was a significant site x depth interaction (*p*=0.0160). Coral recruit assemblages were overall dominated by ephemeral species such as starlet coral *Siderastrea radians* (Pallas 1766) and mustard hill coral *Porites astreoides* (Pallas 1766), representing 33% and 31% of the total coral recruit colony abundance. These were followed by lettuce coral *Agaricia agaricites* (Linnaeus 1767), brain coral *Diploria strigosa* (Dana 1846), and finger coral *Porites porites* (Pallas 1766), for a combined 16% (Fig. 1).

Shallow reef zone abundance of *S. radians* reached 3.7 and 3.4colonies/m² at PLC and LCS, respectively. Abundance of *P. astreoides* reached 2.9 and 2.2colonies/m² at PLC and LCS, respectively. Middle reef zone abundance of Abundance of *P. astreoides* reached 2.7 and 2.0colonies/m² at PCA and PLC, respectively. *S. radians* reached 2.5colonies/m² at LCS. *P. astreoides* was dominant at the deeper zones of both, PCA and LCS, with 3.5 colonies/m². *Siderastrea radians* was dominant at the deeper zone of LCS with 2.5colonies/m². These corals were largely growing on formerly *O. annularis* species complex dominated habitats. Most of the dominant reef-building corals across these habitats died following the 2005 massive coral bleaching event. Nonetheless, recruits members of the *O. annularis* species complex were very rare across the shelf, and were present only in low and sporadic abundance in deeper waters. Only seven juvenile individuals of *O. annularis*

Mean density ($\#/m^2$) of coral species present across study sites

Species	PCA-I	PCA-II	PCA-III	LCS-I	LCS-II	LCS-III	PLC-I	PLC-II	PLC-III
Gorgonia ventalina	-	-	-	-	-	-	-	-	0.77
Muriceopsis sp.	-	-	-	-	-	-	-	-	0.77
Pseudopterogorgia sp.	-	0.84	-	-	-	-	-	-	-
Plexaura sp.	-	-	-	-	-	-	-	-	-
Plexaurella sp.	-	-	-	-	-	-	0.84	-	-
Eunicea sp.	-	0.84	-	-	-	-	-	-	-
Pseudoplexaura sp.	-	-	-	-	-	0.92	-	-	0.77
Pterogorgia sp.	-	-	-	-	-	-	-	-	-
Briareum asbestinum	-	-	-	-	-	1.85	-	-	-
Acropora palmata	-	-	-	-	-	-	-	-	-
Favia fragum	-	0.84	0.92	-	-	-	-	-	-
Porites astreoides	-	13.43	17.54	10.91	12.93	17.54	14.27	10.00	3.85
Porites porites	-	-	0.92	0.84	0.92	1.85	1.68	2.31	1.54
Porites divaricata	-	-	-	-	0.92	-	-	-	-
Porites furcata	-	-	0.92	-	-	-	-	-	-
Porites branneri	-	-	2.77	-	-	0.92	1.68	0.77	0.77
Siderastrea radians	1.54	7.55	12.00	16.79	11.08	5.54	18.47	5.39	12.31
Agaricia agaricites	-	1.68	7.39	-	-	3.69	5.04	1.54	3.85
Agaricia tenuifolia	-	-	1.85	1.68	-	-	-	-	2.31
Agaricia fragilis	-	-	-	-	-	-	-	-	-
Agaricia humilis	-	0.84	0.92	-	1.85	-	-	-	-
Diploria strigosa	-	1.68	3.69	0.84	1.85	1.85	2.52	0.77	-
Diploria labyrinthiformis	-	-	-	0.84	-	-	-	-	-
Colpophilia natans	-	-	-	0.84	-	-	-	-	-
Meandrina meandrites	-	0.84	-	-	-	-	0.84	-	2.31
Orbicella annularis	-	-	-	-	-	-	-	0.77	1.54
Orbicella faveolata	-	-	0.92	-	-	-	2.52	-	2.31
Orbicella franksi	-	-	-	-	-	-	-	-	0.77
Montastraea cavernosa	3.08	-	-	0.84	-	0.92	-	-	1.54
Dichocoenia stokesii	-	-	-	-	-	-	-	-	0.77
Eusmilia fastigiata	-	1.68	0.92	-	-	-	-	-	-
Millepora alcicornis	1.54	1.68	1.85	-	1.85	0.92	-	0.77	1.54

(2%) and 3 of *O. faveolata* (0.9%) were documented out of the 347 recruit colonies found across the 465 surveyed quadrats, suggesting that natural population recovery seven years following the massive post-bleaching coral mortality in 2005-2006 was still very limited for this critically-important reef-building species complex.

Total coral recruit density was significantly different among sites (p=0.0020), but not among depth zones (Fig. 2a). The highest overall densities were documented at the deeper zones of PCA and LCS, with 10.5colonies/m^2 and 7.2colonies/m^2, respectively. The highest density of the middle depth zone was observed at PCA with 6.4colonies/m^2, while the highest density of shallower zones was observed at LCS with 9.6colonies/m^2. Coral species richness was significantly different among sites (p=0.0130), particularly between PCA and LCS (p=0.0070), and between PCA and PLC (p=0.0130) (Fig. 2b). No significant difference among depth zones was observed. The highest species richness was at deeper zones of PCA

TABLE 2

Two-way ANOSIM test of spatial variation in coral recruit community structure and biodiversity patterns

| Parameter	Community structure		Species richness		H'n		J'n	
	Global R	p	Global R	p	Global R	p	Global R	p
Site	0.034	**0.0260**	0.046	**0.0130**	0.029	**0.0420**	0.010	0.1960
PCA-LCS	0.077	**0.0060**	0.084	**0.0070**	0.046	0.0550	0.013	0.2040
PCA-PLC	0.028	0.1280	0.085	**0.0130**	0.067	**0.0320**	0.038	0.0900
LCS-PLC	0.011	0.2230	-0.021	0.9310	-0.016	0.8320	-0.014	0.7880
Depth (m)	0.008	0.7040	0.005	0.2860	0.014	0.1550	0.023	0.0880
<5 m vs 5-10 m	-0.012	0.6790	-0.020	0.8590	-0.012	0.6150	-0.011	0.5830
<5 m vs 10-15 m	-0.022	0.8850	-0.007	0.2830	0.014	0.1870	0.022	0.1230
5-10 m vs 10-15 m	0.006	0.2970	0.026	0.0880	0.035	0.0620	0.049	**0.0310**
Site x Depth	0.052	**0.0160**	0.032	0.0950	0.023	0.1570	0.019	0.20
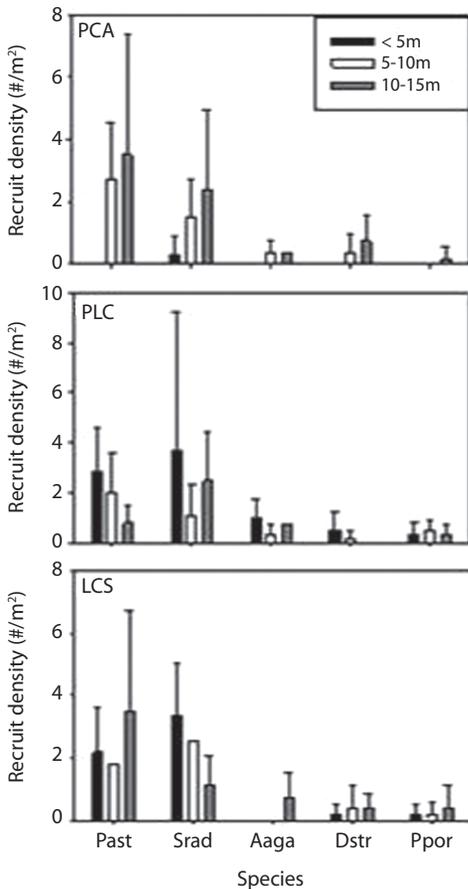
Fig. 1. Coral recruit density (#/m²) of the overall five more abundant coral species (mean±95% confidence interval). Past= *Porites astreoides*, Srad=*Siderastrea radians*, Aaga= *Agaricia agaricites*, Dstr= *Diploria strigosa*, Ppor= *Porites porites*.

(2.9/transect), PLC (2.6/transect), and LCS (2.2/transect). H'n was significantly different among sites (*p*=0.0420), particularly between PCA and PLC (*p*=0.0320) (Fig. 2c). The highest H'n was documented at deeper zones of PCA (0.8912) and PLC (0.7385), followed by the shallow zone of PLC (0.7385). J'n was significantly different between shallow and deep zones (*p*=0.0310) (Fig. 2d). No site-specific effects were observed. The highest J'n was observed at the deeper zones of PLC (0.7281), PCA (0.6830), and LCS (0.6725).

Percent macrocalgal cover showed no significant differences among sites or depth zones. Highest values were documented at the shallow zone of PCA (25.7%), followed by the middle (23.2%) and deeper depth zone (17%) of LCS (Fig. 3). Most macroalgae were Phaeophytes dominated by *Dictyota* spp. and *Lobophora variegata* Lamouroux 1817. There was a highly significant non-linear negative correlation (r²=0.6864, p<0.0001) between increasing percent macroalgal cover and declining coral recruit density (Fig. 4). PCO analysis showed four general clustering patterns of coral reef bottoms, with one cluster largely dominated by *P. astreoides* recruits, and in a lesser degree by *Montastraea cavernosa* Linnaeus 1767, and *Agaricia tenuifolia* Dana 1846 (Fig. 5). A second cluster was determined by abundant *S. radians* recruits, followed by *A. agaricites* and *D. strigosa*. A third cluster was dominated by
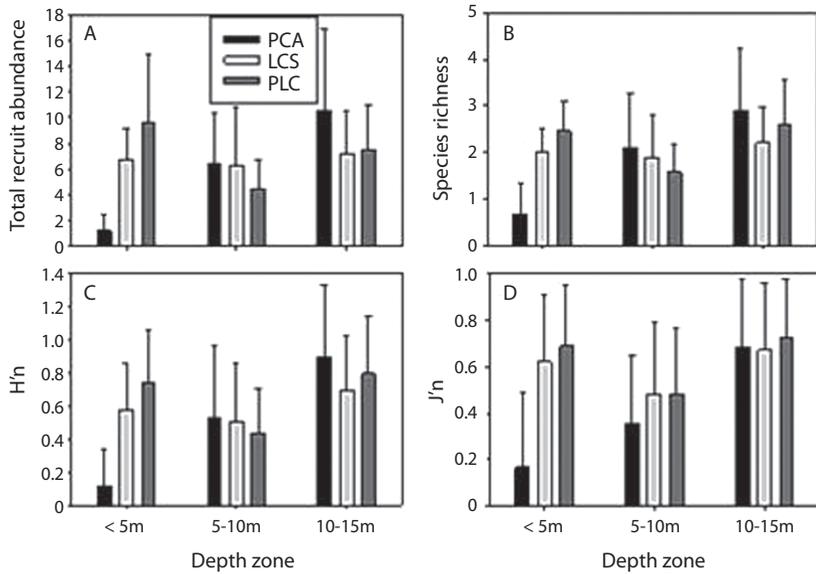
Fig. 2. Coral recruit community metrics (mean±95% confidence intervals): A) Total coral recruit abundance (#/m^2), B) Species richness, C) H'n, D) J'n.
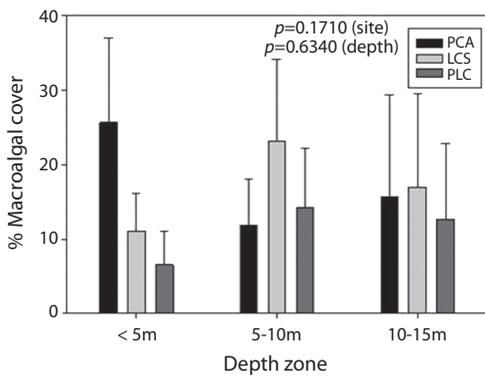
Fig. 3. Percent macroalgal cover (mean±95% confidence interval).
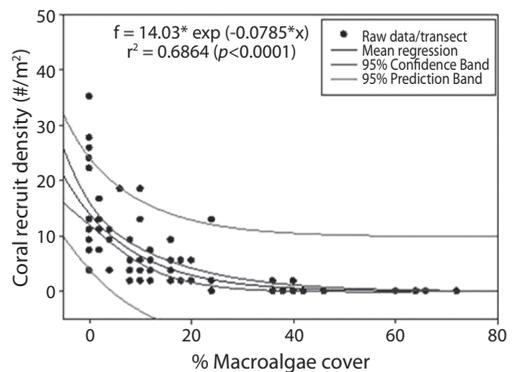
Fig. 4. Non-linear regression of coral recruit density as a function of percent macroalgal cover.

P. astreoides. A final cluster was dominated by open reef bottoms largely devoid of corals, and dominated by brown macroalgal overgrowth.

DISCUSSION

Coral recruit communities at remote Mona Island showed low densities and dominance by short-lived brooder coral species seven years after the 2005-2006 massive bleaching event and the subsequent post-bleaching mass coral mortality. Differences in coral recruit community structure can be attributed to slight variation in percent macroalgal cover as study sites had nearly similar benthic spatial heterogeneity. Nonetheless, trends in dominance by ephemeral coral species were widespread across all study sites. Recovery of largely declining massive reef-building species such as the *O. annularis* species complex was very
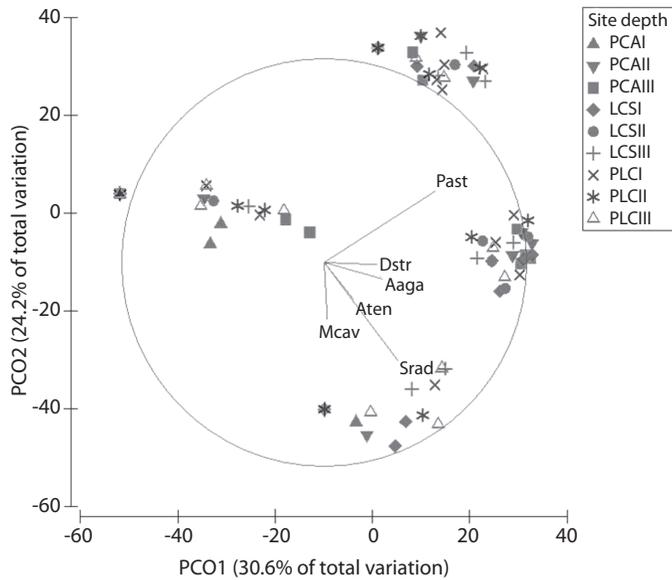
Fig. 5. Principal component ordination (PCO) of coral recruit abundance per site and per depth zone.

limited and even non-existent across extensive reef zones. Instead, dead coral surfaces were largely overgrown by unpalatable brown macroalgae *L. variegata* and *Dictyota* spp. Red encrusting algae *Peysonnellia* spp. were also abundant. Mona's isolated reef systems have followed a transitional trajectory leading to a major phase shift favoring macroalgae and non-reef building, ephemeral coral taxa. Lack of coral reef recovery following major disturbances, including climate change, has been a concerning phenomenon across the Caribbean (McClanahan & Muthiga, 1998; Aronson et al., 2002; Gardner et al., 2003; 2005; Rogers, 2013), and might have significant long-term ecological and socio-economic consequences (Buddemeier et al., 2008; 2010; Paddack et al., 2009; Lane et al., 2013), including regional-scale declines in coral cover and reef complexity (Alvarez-Flip et al., 2011). We suggest that lack of net recovery in remote Mona Island's reefs could be the combined result of several mechanisms involving climate change-related post-bleaching mass coral mortality, chronic YBD disease outbreaks, rapid substrate dominance and out-competition of remnant corals by brown unpalatable macroalgae, declining

herbivory due to long-term fishing impacts, lack of *D. antillarum* population recovery, altered microbial communities associated with crustose coralline algae (CCA) that may negatively affect coral larval settlement cues, and Mona Island's reefs limited connectivity to other reef systems which highly limits potential successful larval recruitment from other locations.

The observed trend of low coral recruit densities and dominance by short-lived brooder coral species is very similar to recent observations from other Caribbean reefs where massive reef-building species have largely declined and have shown limited or no net recovery (Rogers & Miller, 2006; Miller et al., 2009; Hernández-Pacheco et al., 2011; Edmunds, 2013), which suggest a long-term coral recruitment decline across the region. Mean coral recruit density ranged from 1.2 to $10.5/m^2$ at PCA, 6.3 to $7.2/m^2$ at LCS, 4.5 to $9.5/m^2$ at PLC in our study. But earlier studies across the wider Caribbean showed higher recruit density values than most recent accounts. Bak and Engel (1979) documented coral recruit densities of $16.8/m^2$ across the 3-9m depth zone, and of $12.9/m^2$ across the 9-17m depth zone at Curaçao. Rogers et

al. (1984) found coral recruit densities ranging from 13 to 42colonies/m^2 at Salt River Canyon, St. Croix, USVI across depth ranges similar to this study. Carpenter and Edmunds (2006) also found coral recruit colony densities of 6.2/m^2 at Belize, 26.7/m^2 at St. Croix, 28.9/m^2 at Barbados, 26.6/m^2 at Port Antonio, 15.6/m^2 at Bonaire, and 33.8/m^2 at Grenada. They also found that highest coral recruit densities correlated with high densities of *D. antillarum* and lower percent algal cover. Tomascik (1991) documented relatively common recruits of *O. annularis*, *Siderastrea siderea* (Ellis & Solander, 1786), and *Diploria* spp. on settlement plates from non-polluted reefs at Barbados. Bak and Meesters (1999) also found relatively common juvenile colonies of *O. annularis* species complex, *S. siderea*, and other massive coral species at Curaçao. There has also been evidence that fishing management can strongly indirectly influence coral recruitment dynamics. Mumby et al. (2007) documented coral recruit densities ranging from 10 to 14/m^2 within a no-take marine protected area (MPA), and from 4.5 to 6/m^2 across non-MPA sites at Exuma Cays, Bahamas. But large massive Caribbean-wide disturbances, such as recurrent massive bleaching events in 1987, 1998, and 2005 (Eakin et al., 2010), recurrent mass coral disease outbreaks (Weil, 2004), and the mass mortality of *D. antillarum* (Lessios, 1988) have resulted in a major transition in the ecological state of coral reefs. A key characteristic of such a change has included rapidly declining coral recruit densities.

Recent studies have documented declining coral recruit densities across the Caribbean. Irizarry-Soto and Weil (2009) found a decline from 4.8 to 2.8 coral recruit colonies/m^2 between 2003 and 2005, and very low recruit abundance of massive reef-building species in La Parguera, Puerto Rico. Coral recruit density within a no-take MPA in Exuma Cays, Bahamas, increased from approximately 3.8/m^2 for *P. astreoides*, 1.4/m^2 for *A. agaricites*, and 2.1/m^2 for *O. annularis* in 2004 to 8.4/m^2, 2.3/m^2, and 3.1/m^2 in 2007 for each species, respectively (Mumby & Harborne,

2010). Coral recruit density outside the MPA shifted from 2.8/m^2 in 2004 to 3.5/m^2 in 2007 for *P. astreoides*. Densities of 0.6/m^2 for *A. agaricites* and 2.2/m^2 for *O. annularis* in 2004 showed no significant change outside the MPA by 2007. Even recent studies from Mona Island have shown a 30-80% loss of *O. annularis* and *O. faveolata* due to YBD outbreaks (Bruckner & Bruckner, 2006), failed recruitment, minimal re-sheeting, and exposed skeletal surfaces largely colonized by macroalgae, bioeroding sponges, and hydrocorals (Bruckner & Hill, 2009). Ongoing studies at Mona Island have preliminarily suggested that a stunning 96% of large-sized colonies of *O. annularis* species complex across the same surveyed sites in this study were either killed or are showing partial mortality due to YBD infections (Hernández-Delgado, unpublished).

Rapidly declining coral recruitment and lack of coralline community recovery across the Caribbean significantly contrasts recovery trends documented in isolated coral reefs off Western Australia where coral cover increased from 9 to 44% within 12 years of the 1998 massive coral bleaching event by a combination of coral tissue regeneration of remnant surviving colonies and coral recruitment (Gilmour et al., 2013). Diaz-Pulido et al. (2009) also documented rapid reef regeneration following the 2006 coral bleaching-related mass mortality across the Great Barrier Reef due to rapid regeneration rates of remnant coral tissue, strong coral out-competition of *L. variegata*, a natural seasonal decline in macroalgal dominance, and an effective MPA system. However, the benefits from MPAs may not be great enough to offset the magnitude of losses from acute thermal stress events (Hughes et al., 2011; Selig, Casey & Bruno, 2012) if such impacts operate in combination with other local human-driven factors, including herbivore overfishing (Mumby & Harborne, 2010).

We argue that shifting benthic community trajectories have largely impacted coral recruitment dynamics. The observed shift in coral recruit biodiversity is a consequence of the massive post-bleaching coral mortality in

2005-2006 and has resulted in a transitional shift in benthic community trajectory under increasing stress associated to climate change favoring non-reef building taxa. Large-scale (temporal, spatial) massive coral bleaching episodes can lead to significant mortality by post-bleaching disease outbreaks (Miller et al., 2006; 2009), which can potentially lead to a dramatic loss of coral reproductive potential (Weil et al., 2009), the onset of Allee effects, and to reproductive failure (Connell, 1997). Coral recruits exhibit an apparent tolerance to massive bleaching (Mumby, 1999), but evidence of long-term survival following such disturbances is still very limited. Weil et al. (2009) observed that YBD had deleterious impacts on sexual reproduction in *O. faveolata*. Significant physiological fragmentation in *O. annularis* and *O. faveolata* colonies from Culebra Island, Puerto Rico, resulted in permanently halting sexual reproduction in fragmented remnants since the 2005 bleaching episode (Hernández-Delgado, unpublished), similarly to declining reproduction in coral physiological fragmentation experiments documented elsewhere (Szmant-Froelich, 1985; Szmant, 1986; 1991; Szmant & Gassman, 1990; Soong 1993). There is also evidence from the eastern Pacific that most of the recruitment following a massive bleaching and mortality event occurs largely due to rapid recruitment of ephemeral, high-recruiting coral taxa which can be different in comparison to the pre-existing coral community (Medina-Rosas, Carriquiry & Cupul-Magaña, 2005). Therefore, a shift in benthic community structure trajectory such as the one documented in Mona Island implies a change from dominance by engineer species to ephemeral, poor reef builders. Under current and forecasted climate change trends (Hoegh-Guldberg, 1999), and under current declining population trends in *O. annularis* (Hernández-Pacheco et al., 2011), the future trajectories of coral reefs may be significantly compromised.

We also argue that shifting herbivory dynamics, in combination with natural eutrophication pulses, may indirectly affect coral recruitment dynamics due to algal out-competition of corals. Severely depleted *D. antillarum* populations, as well as low abundance of large sized fish herbivores (Scaridae), across the Mona Island shelf (Hernández-Delgado unpublished), and grazing preferences of remnant grazer guilds (Szmant, 2002) is probably associated to the significant shift in dominance by *L. variegata* and *Dyctiota* spp., which in turn are significantly affecting coral larval recruitment. Low herbivory of unpalatable brown macroalgal assemblages is a critical factor that may trigger further coral decline due to out-competition of adult corals, and preemptive out-competition of coral spat. Both *L. variegata* and *Dictyota* spp. (Box & Mumby, 2007), and *Ramicrusta* spp. (Eckrich & Engel, 2013) can strongly out-compete juvenile corals due to shading and abrasive effects, or inhibit successful coral larval recruitment. Kuffner et al. (2006) also found experimental evidence that the combined presence of intermingled unpalatable brown macroalgae and cyanobacteria caused either recruitment inhibition, avoidance behavior or larval mortality in multiple coral species. Further, we propose that natural nutrient enrichment pulses can fuel up algal growth. Physical meso-scale oceanographic processes such as internal waves or seiches (Wolanski & Delesalle, 1995; Leichter, Shellenbarger, Genovese & Wing, 1998) and gyre currents (Corredor et al., 2004), in combination with local-scale micro-upwelling associated to strong tidal currents (Shea & Broenkow, 1982), may bring up deep, nutrient-rich waters towards Mona's narrow shelf. Also, groundwater infiltration might contribute natural nutrient pulses further triggering macroalgal (Lapointe, O'Connel & Garrett, 1990) and cyanobacterial blooms (Littler, Litter, Lapointe & Barile, 2006). Mona Island is a carbonate platform with extensive cave systems and groundwater flows documented to occur even at 20-30 m depths (Hernández-Delgado, personal observations). These factors clearly suggest that management of herbivory is critical for the conservation of coral reef resilience and coral recruitment dynamics.

Hughes and Connell (1999) found that coral reef assemblages that are similar in coral community composition, but under different management regimes may show profound differences in recruitment dynamics and species turnover, with major implications for their ecology, evolution and management. Fully functional no-take MPAs and recovering populations of *D. antillarum* and fish herbivore guilds seem to have a significant role in fostering increased coral recruitment rates. According to Mumby et al. (2007), coral recruit density can increase up to 2-fold within no take MPAs as a result of reduced fishing pressure and weak predator–prey interactions that can create trophic cascades that increase the abundance of grazing fishes and reduce the coverage of macroalgae on coral reefs, therefore opening new substrate for coral larvae. Carpenter and Edmunds (2006) found that population recovery of *D. antillarum* is occurring at both local and regional scales, and that urchin grazing is creating conditions favoring coral recruitment. Nonetheless, *D. antillarum* recovery in Puerto Rico has been patchy and spatially limited even three decades after mass mortality (Ruiz-Ramos, Hernández-Delgado et al., 2011). Long-term trends documented in Mona Island and elsewhere around Puerto Rico have also shown that brown macroalgae have become the dominant component of many coral reefs (Hernández-Delgado, 2005; Ballantine et al., 2008; García-Sais et al., 2008). If macroalgae dominate open available substrates, they might permanently inhibit coral recruitment either due to direct out-competition or by overgrowing CCA, and in the long run affect coral reef recovery ability from disturbance (McCook, Jompa & Díaz-Pulido, 2001). CCA are key reef-building primary producers known to induce the metamorphosis and recruitment of many species of coral larvae (Negri, Webster, Hill & Heyward, 2001). Reef biofilms (particularly microorganisms associated with CCA) are also important as settlement cues for multiple marine invertebrates, including corals (Wieczorek & Todd, 1998). CCA is highly vulnerable to macroalgal overgrowth as well as to

increasing SST. Webster et al. (2011) provided solid experimental evidence that rapid loss of CCA-covered surfaces and its associated biofilms resulted in a massive failure of coral recruitment due to the permanent effects on CCA's photo-physiology and its inability to produce natural chemical cues for larval recognition. Coral reefs require high levels of grazing intensity to prevent further macroalgal blooms from taking place, and to reopen reef substrate to increasing percent CCA cover to trigger increased coral larval recruitment. Therefore, reversing low herbivory should be a critical component to improve coral recruitment success.

Natural recovery of remote coral reefs may seem increasingly difficult due to regional scale of ecosystem decline across the Caribbean which compromise natural connectivity to other reefs Lack of coral reef recovery also implies declining coral functional redundancy and coral reef ecosystem resilience, which could in turn result in a long-term decline in ecological scales of connectivity. Coral reefs at Mona Island are high-circulation, oligotrophic, oceanic reef systems, located far from known anthropogenic pollution sources, but also far from potential source coral reefs. Therefore, genetic isolation due to the oceanographic barrier associated to strong surface currents across the Mona Channel between La Hispaniola and Puerto Rico play a critical role in maintaining high genetic structuring and rendering isolated coral reefs to largely rely on remnant colony regrowth, colony fragmentation, and self-recruitment for their natural recovery from disturbance. Long-distance coral larval dispersal is an unusual event (Baums et al., 2005; 2006; Vollmer & Palumbi, 2007; García-Reyes & Schizas, 2010; Mège et al., 2014) and suggest the paramount importance of replenishing rapidly declining coral reefs though a combination of novel efforts focused on ecosystem-based approaches (i.e., managing food webs, enhancing herbivory, increasing percent cover CCA, and improving coral reproductive stocks).

Replenishment of depleted coral engineer species will require immediate novel efforts (i.e., low-tech coral farming) to rehabilitate their populations. It will also require large-scale, ecosystem-based management of reef fisheries to foster the rehabilitation of the entire food web, with particular attention of recovering herbivore guilds. Alternatives such as propagating and restocking *D. antillarum* populations should be implemented across shelf-wide scales. These will represent important steps towards fostering improved self-recruitment and buying critical time for rapidly declining coral reefs to rehabilitate ecosystem resilience and cope with increasing climate change impacts. Failing to recognize the importance of recovering herbivory, reducing brown macroalgal cover, increasing crustose coralline algae (to foster increased coral recruitment), and propagating key reef-building coral species may result in losing the last opportunity of saving coral reefs in a transitional state from falling into an alternative, irreversible ecological collapse.

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RESUMEN

Patrones a gran escala del reclutamiento de coral en Isla Mona, Puerto Rico: evidencia de una trayectoria transitoria de comunidad después del blanqueamiento y mortalidad coralino masivo. Los arrecifes de coral han disminuido en gran medida en el noreste del Caribe después de los blanqueamientos y muerte masiva de coral en el 2005. El calentamiento superficial del mar relacionado con el cambio climático y brotes de enfermedades en corales como el sindrome de plaga blanca y la enfermedad de banda amarilla (YBD) han causado una disminución significativa de coral de arrecife afectando las especies constructoras de coral (es decir, el complejo de especies *Orbicella annularis*) que no muestran signos evidentes de recuperación a través del reclutamiento larval sexual. Nos centramos en las densidades de coral recluta en tres sitios de coral espuela y surco a lo largo de la plataforma occidental de la remota Isla de Mona, Puerto Rico: Punta Capitán (PCA), Pasa de Las Carmelitas (PLC) y Las Carmelitas-Sur (LCS). Los datos fueron recolectados durante noviembre de 2012 a lo largo de 93 transectos a través de tres zonas de profundidad (<5m, 5-10m, 10-15m). Se documentaron un total de 32 especies de corales (9 octocorales, 1 hidrocoral, 22 scleractinios) entre la comunidad coral recluta. Comunidades de coral recluta mostraron bajas densidades y predominancia por especies criadoras rápidas durante siete años después del evento del 2005. La densidad coral recluta varió entre 1.2 y $10.5/m^2$ en el PCA, 6.3 y $7.2/m^2$ en LCS, 4.5 a $9.5/m^2$ en el PLC. Diferencias en la estructura de la comunidad coral recluta pueden atribuirse a la ligera variación en el porcentaje de cobertura de macroalgas y composición en los sitios de estudio que tenían una heterogeneidad espacial bentónica muy similar. Tendencias en el predominio de las especies de coral efímeras fueron generalizadas. Recuperación de especies de arrecife con alta disminución como la especie *O. annularis* del complejo de especies fue muy limitado e incluso inexistente a través de zonas extensas de arrecife. La falta de recuperación puede ser el resultado combinado de varios mecanismos que implican cambio climático, brotes crónicos de YBD, macroalgas, pesca, erizos y conectividad limitada de los arrecifes de la isla Mona a otros sistemas de arrecife. También hay una necesidad de impulsar la rehabilitación de la estructura trófica de peces, con énfasis en la recuperación de gremios herbívoros y las poblaciones agotadas de *D. antillarum*. Al no reconocer la importancia de la gestión de rehabilitación y capacidad de recuperación basado en los ecosistemas se estima que la recuperación de arrecifes de coral es muy improbable.

Palabras clave: Cambio climático, disminución de coral, reclutamiento, trayectoria de comunidad, isla Mona, Puerto Rico, estado transitorio

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