

Bomb-cratered coral reefs in Puerto Rico, the untold story about a novel habitat: from reef destruction to community-based ecological rehabilitation

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Abstract: Ecological impacts of military bombing activities in Puerto Rico have often been described as minimal, with recurrent allegations of confounding effects by hurricanes, coral diseases and local anthropogenic stressors. Reef craters, though isolated, are associated with major colony fragmentation and framework pulverization, with a net permanent loss of reef bio-construction. In contrast, adjacent non-bombarded reef sections have significantly higher benthic spatial relief and biodiversity. We compared benthic communities on 35-50 year-old bomb-cratered coral reefs at Culebra and Vieques Islands, with adjacent non-impacted sites; 2) coral recruit density and fish community structure within and outside craters; and 3) early effects of a rehabilitation effort using low-tech Staghorn coral *Acropora cervicornis* farming. Reef craters ranged in size from approximately 50 to 400m² and were largely dominated by heavily fragmented, flattened benthos, with coral cover usually below 2% and dominance by non-reef building taxa (i.e., filamentous algal turfs, macroalgae). Benthic spatial heterogeneity was lower within craters which also resulted in a lowered functional value as fish nursery ground. Fish species richness, abundance and biomass, and coral recruit density were lower within craters. Low-tech, community-based approaches to culture, harvest and transplant *A. cervicornis* into formerly bombarded grounds have proved successful in increasing percent coral cover, benthic spatial heterogeneity, and helping rehabilitate nursery ground functions. Rev. Biol. Trop. 62 (Suppl. 3): 183-200. Epub 2014 September 01.

Key words: Benthic community structure, bombing impacts, community-based ecological rehabilitation, coral reefs, fish community structure, military activities, novel habitats.

Long-term adverse ecological impacts of military maneuvers on coral reef ecosystems have remained as a concern as there is still limited information in the literature about impacts across multiple spatial and temporal scales. Most studies have often focused on very large spatial scale assessments, which have by default often overlooked some of the acute impacts on bomb-cratered coral reefs at smaller (i.e., fringing reef) spatial scales. Most published accounts were from studies conducted at Vieques Island, Puerto Rico (Raymond, 1978; DON 1979; DON 1980; DON

1986, Raymond & Dodge, 1980; Antonius & Weiner, 1982; GMI, 2003; GMI, 2005, Deslarzes, Nawojchik, Evans, McGarrity & Gehring, 2006; Evans, Nawojchik & Deslarzes, 2006; Hernández-Cruz, Purkis & Riegl, 2006; Kendall & Eschelbach, 2006; McGarrity & Deslarzes, 2006; Riegl, Moyer, Walker, Kohler, Gilliam & Dodge, 2008; Bauer, Menza, Foley & Kendall, 2008; Bauer & Kendall, 2010) which were conducted over island wide spatial scales and found minimal destructive ecological impacts of bombing activities at such large scales, concluding that hurricanes and multiple



localized human stressors (i.e., sedimentation, fishing) caused significant confounding effects. Even studies which have documented critical acute impacts of bombing and sedimentation across military-impacted coral reefs (IDEA, 1970; Carrera-Rodríguez, 1978; Rogers, Cintrón & Goenaga, 1978; Goenaga, 1986; Goenaga, 1991) did not provide a full quantitative characterization of the localized impacts on bomb-cratered reefs at reef-level spatial scales. None of these studies had either the temporal resolution to address long-term recovery of impacted sites. Therefore, the impacts of habitat fragmentation at across reef spatial scales associated to military activities and its long-term consequences on the recovery ability of local community structure and ecosystem resilience have still been poorly addressed.

Localized bombing impacts on coral reefs still remain controversial, and most of the literature has focused on blast fishing. This is known to cause extensive reef framework destruction across Indo-Pacific (McManus, Reyes & Nañola, 1997; Pet-Soede & Erdmann, 1998) and Red Sea coral reefs (Riegl, 2001), besides its concomitant overexploitation of fishery resources. Blast fishing impacts have caused significant loss of coral cover, an increase in the amount of bare substrate and rubble, and a decline in fish species richness and abundance (Riegl & Luke, 1999). These authors suggested that natural regeneration of impacted reef communities is likely to be very slow, possibly taking several hundred years, and that rehabilitation would be difficult since coral transplants would have to mimic the previously existing community. The frequency and magnitude of military bombing activities in Vieques Island showed a steady significant increase during the cold war years. Rosa-Serrano (1996) documented increasing crater abundance within bombarded areas between 1964 and 1988 using GIS-based analysis, suggesting a long-term increase of physical impacts of bombing. Porter (2000) found unexploded ordnance, leaking toxic 2-4-6-Trinitrotoluene (TNT) on and around reefs, and over 1,000 deteriorating barrels of unknown chemicals

on the sunken military vessel *USS Killen* off southeast Vieques. Porter, Barton and Torres (2011) also found a statistically significant inverse correlation between the coral species richness, colony abundance and species diversity, and the density of military ordnance across reef scales in Vieques. There were also multiple animals across the reef food web polluted with toxic compounds similar to those present in unexploded ordnance. Chromium in sediments, and TNT in both, water and sediments, exponentially increased within areas still littered with unexploded ordnance.

Reef craters present in both, Culebra and Vieques Islands coral reefs are often very small in comparison to the scale of each island, each ranging in size from approximately 50 to 400m². But these are largely dominated by heavily fragmented flattened benthos, with % coral cover usually below 2% and dominance by non-reef building taxa (i.e., filamentous algal turfs, macroalgae) (Fig. 1a-c). In contrast, adjacent non-bombarded reef zones are still dominated by consolidated benthos, with higher percent living coral cover and larger abundance of reef building species (Fig. 1d-f). Benthic spatial heterogeneity is also significantly lower within crater scales which also results in a lowered functional value as fish nursery ground. The fact that physical disturbance within bombarded grounds was so locally extensive resulted in a mosaic of habitat patches with permanent loss of reef framework and in potentially declining multiple ecosystem functions and services. Therefore, reef craters have become a *de facto* novel habitat, and as such, there is a need to address the ecological status of benthic and fish communities, as well as their recovery state three to five decades after bombing.

This study was aimed at: 1) documenting the condition of benthic communities within 35-50 year-old reef craters at Culebra and Vieques Islands, Puerto Rico, in comparison to adjacent non-bombarded sites within former military maneuver sites; 2) comparing coral recruit density and fish community structure within and outside reef craters; and

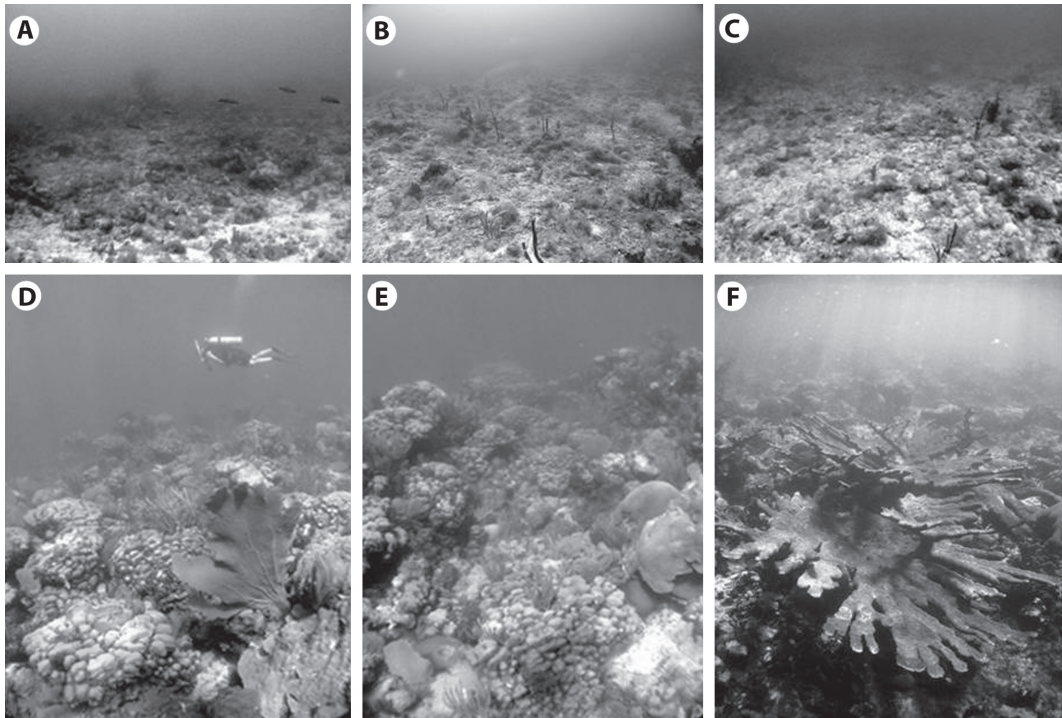


Fig. 1. Benthic community structure within bomb-cratered and non-impacted reefs. A-B) Reef craters dominated by low spatial relief and brown macroalgae *Dictyota* spp.; C) Reef crater dominated by filamentous algal turf; D-E) Non-impacted forereef terrace dominated by *Montastraea* (= *Orbicella*) *annularis* species complex; F) Shallow non-impacted reef with remnant patch of *Acropora palmata*.

3) addressing the preliminary impacts of a community-based bombarded coral reef rehabilitation effort using low-tech approaches to cultivate threatened staghorn coral, *Acropora cervicornis* (Lamarck, 1816), and rehabilitate bombarded coral reefs.

MATERIALS AND METHODS

Study sites: Studies were conducted across 15 fringing reef sites, 11 at Culebra Island (located between 18°19.791'N, 65°19.943'W and 18°20.776'N, 65°20.498'W) and 4 at Vieques Island (located between 18°08.784'N, 65°18.482'W and 18°09.698'N, 65°25.073'W), off eastern Puerto Rico (State Plane, NAD83, FIPS PR5200, Fig. 2). Reef craters examined in this study ranged between 50 and 400m². Sites were selected based on their representativeness of typical reef segments

impacted by framework destruction as our aim was documenting what is the status of severely impacted reef sites 35-50 years after bombing impacts. Crater age was estimated from aerial photography and from anecdotal accounts from older fisher folks from both islands, and was a key factor for selecting impacted study sites to have a more accurate estimate of reef recovery trends through time. Control sites were selected on adjacent (usually <250m) sites not directly impacted by bombs. Reefs were subdivided by treatment (impacted-craters [n=7], non-impacted controls [n=8]), and depth (shallow, 1-3m [n=9]; deep, 6-10m [n=6]). In Culebra, sampling was conducted in 6 shallow (3 impacted, 3 controls) and 5 deep (2 impacted, 3 controls) reefs. In Vieques sampling was conducted in 2 shallow (1 impacted, 1 control) and 2 deep (1 impacted, 1 control) reefs. All benthic surveys in Culebra were conducted

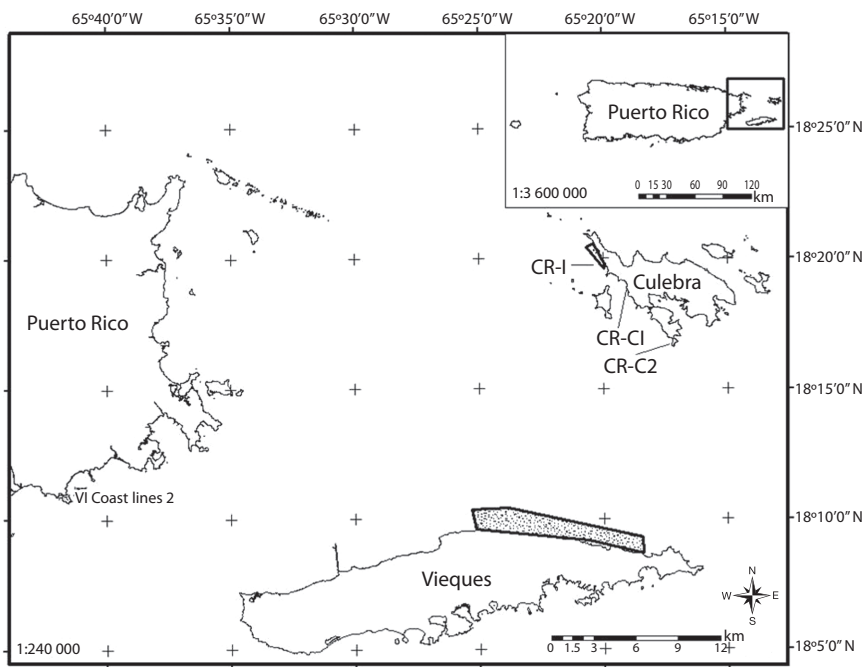


Fig. 2. Study sites in Culebra and Vieques Islands, Puerto Rico. Acronyms are described in the Methods section.

within the Canal Luis Peña no-take Natural Reserve (CLPNR) where all fishing is prohibited. Fish studies were conducted only in Culebra within the CLPNR to reduce confounding factors with fishing impacts elsewhere. Coral recruitment and reef rehabilitation studies were conducted in Culebra at the bombed area described above (CR-I1, CR-I2), at Bahía Tamarindo (CR-C1, 18°18.877'N, 65°19.093'W), and at Punta Soldado (CR-C2, 18°16.846'N, 65°17.192'W). Bahía Tamarindo is also located within CLPNR and was used for artillery training activities and amphibious vehicle landing practices between 1920s and 1950s, but was never bombed. Punta Soldado is located outside CLPNR and was used as a target site during the 1920s but never thereafter. These were used as control sites which underwent different levels of military activities, across different temporal scales, in comparison to direct recent bombing within reef cratered areas at impacted sites until 1970s. Also, these sites are part of a network of coral recruitment monitoring sites.

Benthic community: Benthic habitats were characterized across all sites through 3-6 replicate ten m-long digital video-transects. Number of replicates varied as a function of crater size and covered at least 50-75% of the impacted area within each crater. Transect deployment within each crater was haphazard, often separated by at least 5m. A total of six random, non-overlapping still images/transect were obtained and analyzed with Coral Point Count with excel extensions (v3.6) (Kohler & Gill, 2006) to address percent cover of all benthic components, including coral, algal functional groups (macroalgae, turf, crustose coralline algae [CCA], erect calcareous algae [ECA], *Halimeda* spp.), cyanobacteria, other components, sand, rubble, and bare substrate. A total of 20 random dots per image were used. Coral species richness, species diversity index ($H'n$) (Shannon & Weaver, 1948), and evenness ($J'n$) (Pielou, 1966) were also calculated.

Coral recruits: Coral recruit densities were addressed only in Culebra using triplicate

2.25 x 2m quadrat grids subdivided in 12 replicate 0.75 x 0.50m quadrats/grid from one shallow (CR-IS) and one deep crater (CR-ID), and from two control non-impacted sites at Bahía Tamarindo (CR-C1), and Punta Soldado (CR-C2). High-resolution digital images were collected and all hydrocoral/scleractinian recruits with a diameter below 5cm were counted and identified to the lowest taxon possible.

Fish community structure: Fish communities were characterized only in Culebra using stationary visual censuses within craters (impacted) and adjacent (control) locations following a slight modification from Bohnsack and Bannerot, (1986). Data was collected within a 5 m-radius imaginary cylinder during a period of 15min. All individuals were counted, identified to the lowest taxon possible, and standard fork length was estimated. Size data were used to estimate biomass. Weight-length relationships were calculated following Bohnsack and Harper (1988). Basic information of the fish community structure reported in this study included species richness, abundance, $H'n$, $J'n$, total biomass, and piscivore biomass. Reef structural complexity is known to have an important influence on fish community structure (Roberts & Ormond, 1987). A 6-point scale was used to characterize a reef structural heterogeneity index (RSHI) as follows: 0= no vertical relief; 1= low and sparse relief; 2= low but widespread relief; 3= moderately complex; 4= very complex with numerous caves and fissures; 5= exceptionally complex with high coral cover and numerous caves and overhangs (Hawkins et al., 1999).

Statistical analyses: A three-way permutational analysis of variance (PERMANOVA) was used to test the null hypothesis of no significant difference in benthic biodiversity parameters and community structure between sites (Culebra, Vieques), treatment level (bombarded areas, non-impacted controls), and depth (1-3m, 6-9m) using PRIMER-e v.6.1.14 (Anderson, Gorley & Clarke, 2008). Principal component ordination (PCO) was used

to determine which benthic taxa explained spatial clustering patterns of benthic communities. Proportional data on percent benthic components cover were $\sqrt{}$ -transformed prior to analysis. A one-way PERMANOVA was used to test spatial patterns of coral recruits between bombarded and non-impacted sites in Culebra, followed by PCO. A one-way analysis of similarity (ANOSIM) was used to test spatial patterns of fish communities between bombarded and non-impacted sites in Culebra, followed by a multi-dimensional scaling (MDS) analysis (Clarke & Warwick, 2001). Data were also $\sqrt{}$ -transformed prior to analysis. All tests were based in 10000 permutations. Fish community data also were correlated (Spearman) with RSHI.

Coral reef rehabilitation: A total of 2000 corals were harvested from existing low-tech coral farms through the *Community-Based Coral Aquaculture and Reef Rehabilitation Project* and outplanted to adjacent coral reefs within former military maneuver ranges at two sites in Culebra Island, Bahía Tamarindo and Punta Soldado. Sites selected for outplanting were located within a flat shallow reef (<2.5m) used as artillery maneuver areas at Bahía Tamarindo (impacted site) and at a reef segment at Punta Soldado non-impacted by bombing or artillery maneuvers since 1920s (control site). Corals were attached to masonry nails driven to reef bottom, outplanted in patches of densities ranging from 80 to 120 per 25m². Survival rates and growth were addressed following two representative patches located at elevated rocky outcrops and two patches adjacent to reef sand pockets at increasing time intervals during a year. A two-way ANOSIM was used to test the null hypotheses of no significant change in coral survival rates, skeletal extension, and branch production through time and between sites.

RESULTS

Benthic community: Coral reef benthic communities across bombarded areas showed

TABLE 1
PERMANOVA results of coral reef benthic biodiversity and community structure

Variable	d.f.	Species richness Pseudo-F (<i>p</i>)	H'n Pseudo-F (<i>p</i>)	J'n Pseudo-F (<i>p</i>)	Community structure Pseudo-F (<i>p</i>)
Site	1,13	0.0060 (0.8179)ns*	0.39 (0.5426)ns	2.36 (0.1555)ns	2.18 (0.0473)
Treatment	1,13	11.60 (0.0071)	19.49 (0.0014)	7.24 (0.0252)	2.47 (0.0348)
Depth	1,13	2.33 (0.1432)ns	1.93 (0.1925)ns	0.0061 (0.8079)ns	2.12 (0.0583)ns
Site x Treatment	3,11	3.66 (0.0452)	6.11 (0.0107)	5.24 (0.0174)	1.96 (0.0221)
Treatment x Depth	3,11	6.80 (0.0133)	9.81 (0.0033)	2.31 (0.1366)ns	2.41 (0.0054)
Site x Treatment x Depth	6,8	6.75 (0.0123)	8.32 (0.0044)	2.13 (0.1519)ns	1.95 (0.0122)

*ns= not significant.

significantly more physical destruction and an altered coral assemblage in comparison to control non-impacted sites (Table 1). There was a significantly different benthic community structure between sites ($p=0.0473$) and treatments ($p=0.0348$). Also, interactions between site and treatment, treatment and depth, and among site, treatment and depth were highly significant. Bombarded sites were characterized by having significantly lower coral species richness ($p=0.0452$), percent coral cover ($p=0.0025$), H'n ($p=0.0107$), and J'n ($p=0.0174$) (Fig. 3a-d). Mean coral species richness within bombarded bottoms was 2.2/transect, while mean value at adjacent non-impacted control sites was 8.8/transect. Mean living coral cover within bombarded bottoms was 1.9% and 15.7% at control sites. Coral cover was also higher at deeper (13%) than at shallower sites (6.5%). Mean H'n within bombarded bottoms was 0.4912 and 1.6101 at control sites, while mean J'n within bombarded bottoms was 0.4169 and 0.7834 at control sites. Species richness and H'n also had significant treatment x depth, and site x treatment x depth interactions. Macroalgal cover was higher on control sites (47%), in comparison to bombarded areas (29%), while algal turf was higher within bombarded grounds (26%), in comparison to control sites (16%) (Fig. 1e-f). But none of these differences were significant.

The percent relative cover of the most important reef building coral species was significantly lower within bombarded areas

(Fig. 4). *Montastraea* (= *Orbicella*) *annularis* (Ellis & Solander, 1786) averaged 0.05% within bombarded areas and 4.1% at control sites, while *O. faveolata* (Ellis & Solander, 1786), *O. franksi* (Gregory, 1895), and *M. cavernosa* Linnaeus, 1767 averaged 1.3, 0.5, and 1.0%, respectively, at control sites. None of these species were present within bombarded areas. *Colpophyllia natans* (Houttuyn, 1772) averaged 0.01% within bombarded grounds and 0.38% in control sites. *Diploria strigosa* (Dana, 1846) averaged 0.7% at control sites and was absent within bombarded areas, and *Siderastrea siderea* (Ellis & Solander, 1786) had a mean 0.14% cover within bombarded areas and 1.8% in control sites.

Principal component ordination (PCO) analysis showed two larger clusters of reef communities, and 5 individual sites (Fig. 5). Impacted sites at Culebra were dominated by open substrates composed by a mixture of bare bedrock, rubble and sand pockets (SPR), algal turf, brown macroalgal patches (e.g., *Dicthyota* spp.), and sporadic colonies of octocoral *Pseudopterogorgia* spp. (Fig. 1a-b). Vieques impacted sites were dominated by algal turfs (Fig. 1c). Culebra control site showed a higher spatial heterogeneity mostly dominated by macroalgae, *M. annularis*, and *P. astreoides* (Fig. 1c-d). Control sites at Vieques were also dominated by turf, and in a lesser degree a mixed octocoral community. The proposed PCO solution explained 57% of the observed spatial variation.

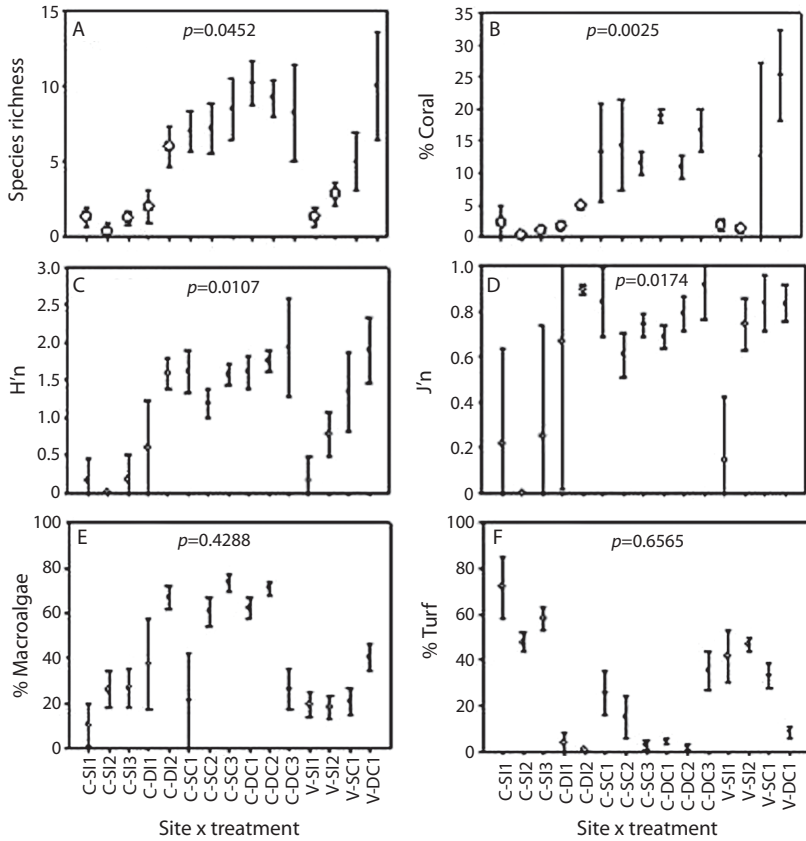


Fig. 3. Benthic community characterization within impacted (open dots) and control sites (black dots) (mean±95% confidence intervals): A) Coral species richness, B) Percent coral cover, C) H'n, D) J'n, E) Percent macroalgae, and F) Percent algal turf. *P* values derived from two-way PERMANOVA (site x treatment effects).

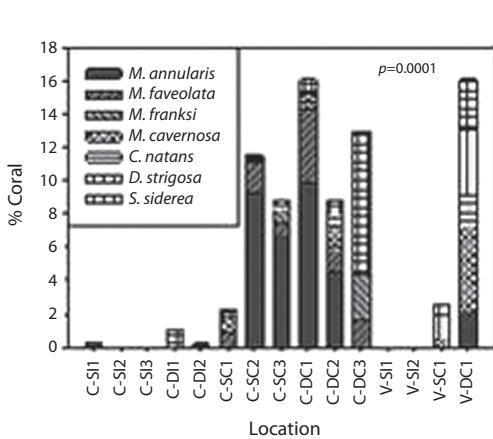


Fig. 4. Percent relative cover of the principal reef-building coral species.

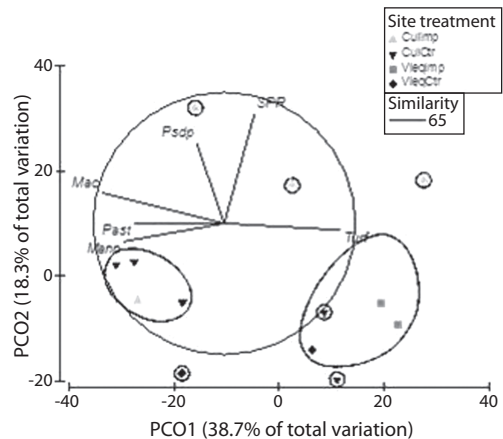


Fig. 5. Principal component ordination (PCO) plot of coral reef benthic communities within bombarded and control reefs. Spatial resolution= 57%. Correlation level of vector selection= 0.65. Similarity cutoff level= 65%.

Coral recruits: Coral recruit density was significantly higher (PERMANOVA, Pseudo-F=6.55, $p=0.0001$) within non-impacted control sites in comparison to bombarded areas. Control site CR-C1 located within CLPNR averaged 51 colonies/30m², while CR-C2 outside CLPNR averaged 21 colonies/30m² (Fig. 6). Impacted site CR-I1 averaged 8 colonies/30m², while CR-I2 averaged less than 3 colonies/30m². Both impacted sites were also located within CLPNR. ANOSIM analysis showed that coral recruit community structure was significantly different between treatments ($R=0.830$, $p=0.0001$). Also, species richness ($R=0.736$, $p=0.0006$), and H'n ($R=0.747$, $p=0.0006$) were significantly higher at control sites than at bombarded areas. No significant difference in J'n was documented. Brooder species such as *Favia fragum* (Esper, 1795), *Siderastrea radians* (Pallas, 1766), and *Porites astreoides* (Lamarck, 1816) were dominant at control sites, while lower abundances of *S. radians* and *P. astreoides* characterized bombarded sites, particularly, at deeper impacted areas. PCO analysis showed five different

clusters of reef communities, and five individual sites (Fig. 7). The three clusters composed of control non-impacted sites were explained by *P. astreoides*, *P. porites*, *F. fragum*, and *Millepora striata* (Lamarck, 1816). Bombarded sites clusters were determined by *S. radians*. The proposed solution by PCO explained 71.1% of the observed spatial variation.

Fish community: Fish community structure also showed significant difference ($p<0.0001$) between treatment levels that were mostly related to a highly significant decline ($p=0.0030$) observed in the reef structural heterogeneity index (RSHI) within bombarded sites (Fig. 8a). RSHI had a mean value of 0.69 within bombarded areas and 2.72 within control sites. Fish species richness was significantly higher (23.4 per count) at control sites ($p=0.0020$) than at bombarded areas (12.6) (Fig. 8b). Fish abundance was also significantly higher ($p=0.0002$) at control sites (491) versus bombarded sites (108) (Fig. 8c). Also, H'n was significantly higher ($p=0.0020$) within control areas (1.6744) in comparison to bombarded

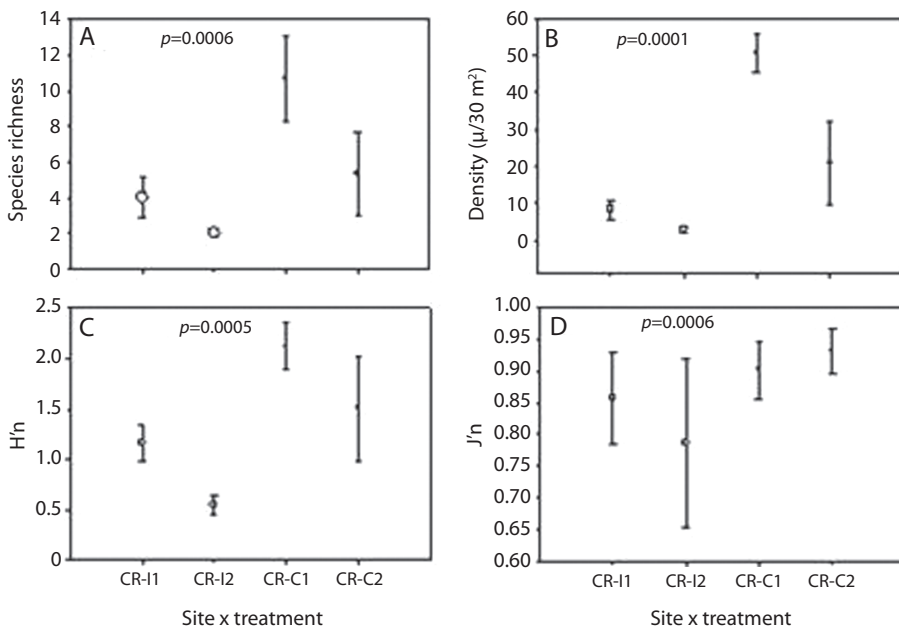


Fig. 6. Coral recruit community parameters at bombarded (open dots) and control non-impacted (black dots) sites in Culebra (mean±95% confidence intervals): A) Species richness, B) Recruit density, C) H'n, and D) J'n.

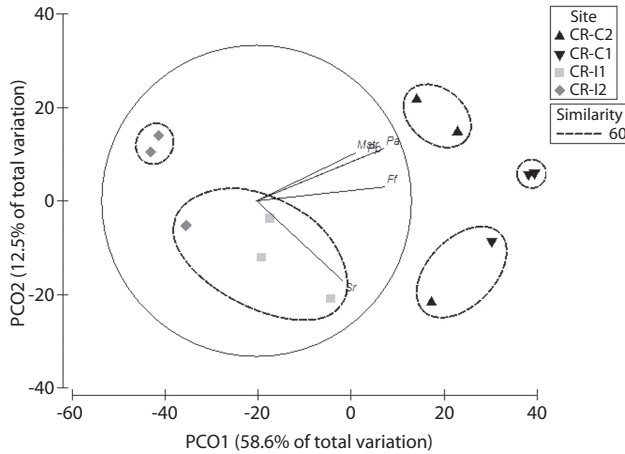


Fig. 7. Principal component ordination (PCO) plot of coral recruit communities within bombed and control reefs. Spatial resolution= 71.1%. Correlation level of vector selection= 0.60. Similarity cutoff level= 60%.

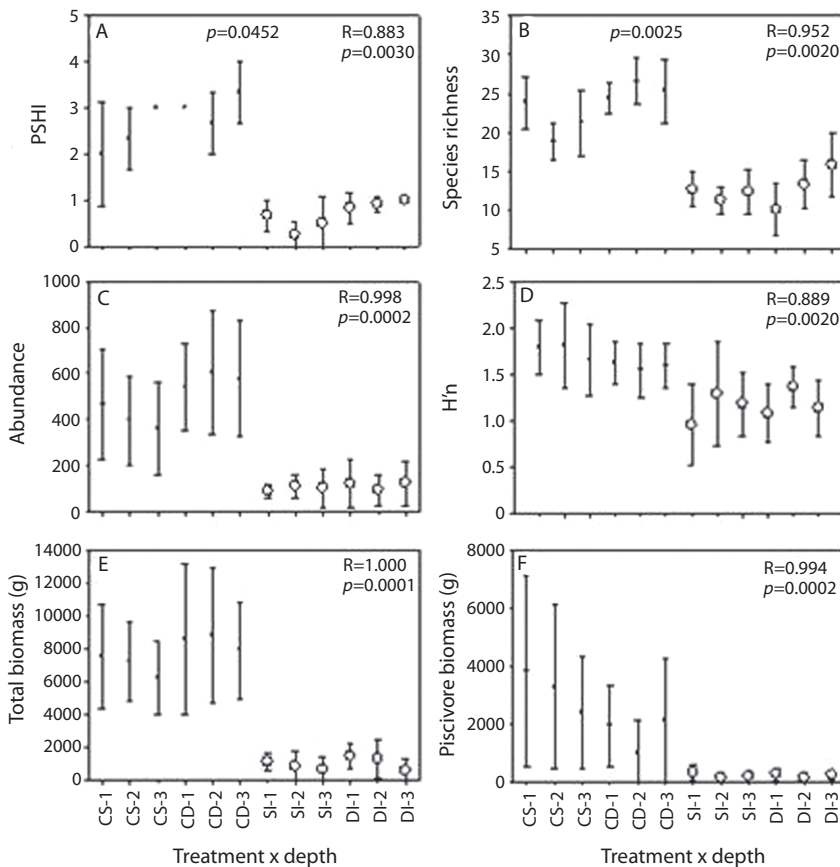


Fig. 8. Fish communities within and outside bombed grounds (mean±95% confidence intervals): A) Reef structural heterogeneity index (RSHI), B) Species richness, C) Abundance, D) Species diversity index ($H'n$), E) Total biomass (g), and F) Piscivore biomass (g). Black dots= bombed grounds, Hollow dots= non-impacted control sites. P values derived from one-way ANOSIM tests. SC= Shallow control, DC= Deep control, SI= Shallow impacted, DI= Deep impacted.

grounds (1.1716) (Fig. 8d). Total fish biomass was significantly higher ($p=0.0001$) at control sites (7 697g) than at bombarded areas (999g) (Fig. 8e). Similarly, piscivore biomass was significantly higher ($p=0.0002$) at control sites (2,406 g) than at bombarded areas (206g) (Fig. 8f). All fish community parameters showed a highly significant linear regression ($p<0.0088$) with RSHI (Table 2), suggesting the strong permanent negative impacts of bombing activities on the demolition of reef framework and the net decline in fish communities associated to losing spatial benthic heterogeneity. Significant reef functional herbivore guilds such as scrapers, including *Scarus iserti* Bloch, 1790, *S. vetula* Schneider, 1801, *Sparisomq viride* (Bonnaterre, 1788), *S. rubiprinne* (Valenciennes, 1839), and *S. radians* (Valenciennes, 1839), and browsers such as *Acanthurus coeruleus* Schneider, 1801 were largely absent from reef craters, in comparison to adjacent non-bombarded sites. Also, important piscivore

guilds such as groupers, including *Epinephelus guttatus* (Linnaeus, 1758), *E. adscensionis* (Osbeck, 1765), *Cephalopholis fulva* (Linnaeus, 1758), and *C. cruentata* (Lacepède, 1802), and snappers *Lutjanus jocu* (Schneider, 1801), *L. analis* (Cuvier, 1828), and *L. apodus* (Walbaum, 1892) were also absent from reef craters. Fishing impacts was not a factor influencing observed differences in fish community structure within and outside craters as fish data were collected from sites located within the no-take CLPNR.

Coral reef rehabilitation: Mean percent colony survival rates of *Acropora cervicornis* outplants was 81% at impacted sites and 86% at control sites after one year, with a mean survival of 88% at impacted sites and 70% at impacted sites on low-relief reef patches adjacent to sand (Fig. 9). Percent survival at elevated rocky outcrops reached 92% at impacted sites and 84% at control sites. Percent

TABLE 2
Linear regression of fish community parameters with the reef structural heterogeneity index (RSHI)

Variable	R	p	Regression equation
Species richness	0.9155	<0.0001	$y = 9.515 + 4.958x$
Abundance	0.9238	<0.0001	$y = 3.401 + 173.2x$
H'n	0.7896	0.0023	$y = 1.075 + 0.2034x$
Total biomass	0.9311	<0.0001	$y = -689.4 + 2949x$
Piscivore biomass	0.7158	0.0088	$y = -142.9 + 848.3x$

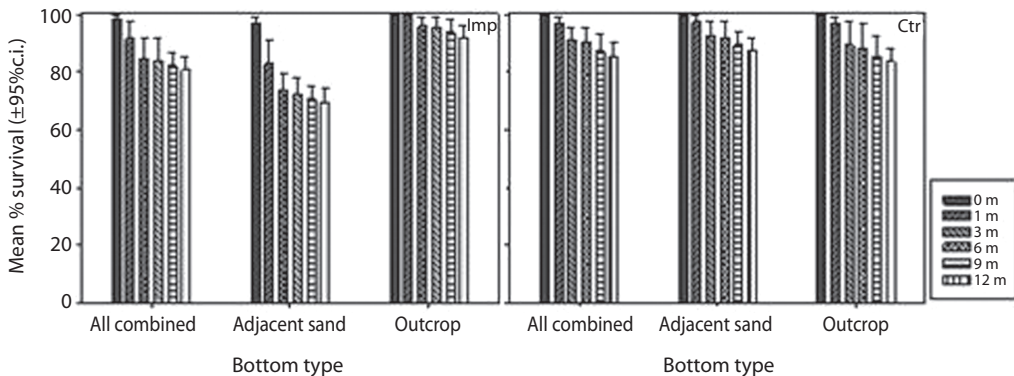


Fig. 9. Mean percent colony survival rate ($\pm 95\%$ confidence intervals) of *Acropora cervicornis* outplants within impacted (Imp) and control (Ctr) sites after one year.

live coral tissue cover on outplanted colonies averaged 85% at both, impacted and control sites after one year (Figure 10a), ranging from 82 to 88% within impacted sites in low-relief patches adjacent to sand and in elevated outcrops, respectively. Mean % live tissue cover ranged from 82 to 89% within impacted sites in low-relief patches adjacent to sand and in elevated outcrops, respectively. Total outplanted colony linear length showed a mean overall increase from 41 to 129cm across impacted sites, and from 32 to 81cm across control sites after one year (Figure 10b). Total outplanted colony branch abundance/colony showed a mean overall increase from 4.5 to 14.4 cm

across impacted sites, and from 3.4 to 8.3cm across control sites after one year (Figure 10c). Temporal effects were significant for all variables, but treatment and position effects were not (Table 3).

DISCUSSION

Profound, acute and persistent negative impacts of historical bombing activities were documented in Culebra and Vieques Islands, Puerto Rico, across coral reef craters spatial scales. Severely impacted reef segments were characterized by having significantly lower spatial relief, bedrock exposure and

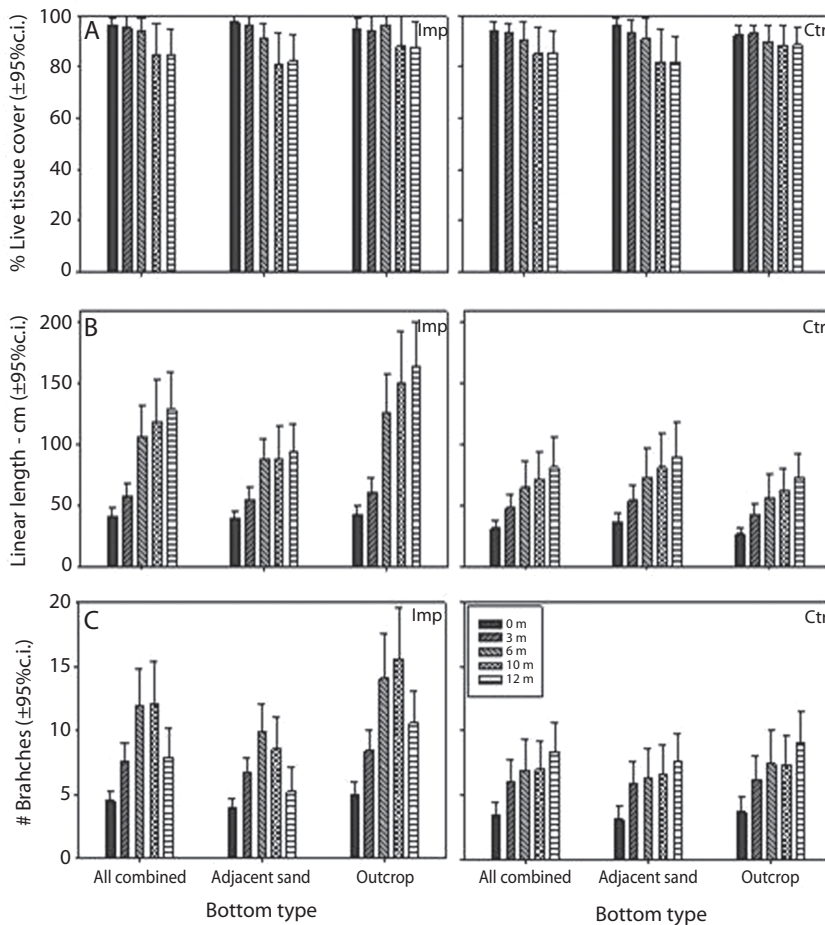


Fig. 10. Outcome of *Acropora cervicornis* outplanting within impacted (Imp) and control (Ctr) sites after one year (mean±95% confidence intervals): A) Percent live coral tissue cover; B) Total linear colony length (cm); C) Branch abundance per colony.

TABLE 3
ANOSIM results of *Acropora cervicornis* outplanting

Variable	Survival	% Cover	Linear length	# Branches
Treatment (0.8630)ns*	R=-0.081 (0.5260)ns	R=0.016 (0.3460)ns	R=0.011 (0.0890)ns	R=0.117
Time (0.0020)	R=0.625 (0.0030)	R=0.576 (0.0020)	R=0.405 (0.0060)	R=0.308
Position (0.3220)ns	R=0.003 (0.1240)ns	R=0.001 (0.5270)ns	R=-0.024 (0.6670)ns	R=-0.046
Treatment x Time (0.0150)	R=0.445 (0.0060)	R=0.565 (0.0060)	R=0.491 (0.0060)	R=0.475
Treatment x Position	R=-0.139 (0.9020)ns	R=0.006 (0.6100)ns	R=-0.058 (0.6690)ns	R=0.020 (0.3720)ns
Time x Position	R=0.733 (0.0010)	R=0.821 (0.0006)	R=0.290 (0.0540)ns	R=0.134 (0.1980)ns

*ns= Not significant.

an abundant mixture of unstable turf-covered rubble and bedrock boulders demolished by explosions. These substrates were also characterized by low coral colony abundance, low percent living coral cover, low coral species richness and H'n, when compared to adjacent control sites. Similarly, coral recruit communities were significantly more depauperate within impacted grounds than in control sites, either within or outside the no-take CLPNR, which suggest the persistent inability of coral recruits to survive the natural oceanographic dynamics of unstable substrates within bombarded sites. This is consistent with severe impacts by blast fishing documented elsewhere (Riegl & Luke, 1999; Riegl, 2001). The permanent lack of natural recovery ability of 35-50 years old bomb-cratered coral reef segments, when compared to adjacent non-bombarded control sites dominated by massive reef-building species such as *M. annularis* species complex, implies that at the local ecosystem scale, bombarded coral reefs have shown a permanent shift in composition and functions, that full recovery of previously existing benthic community structure and spatial heterogeneity may take centuries. Coral recruitment rates of critical reef-building species across the northeast Caribbean region are increasingly low (Rogers, Fitz, III, Gilnack,

Beets & Hardin, 1984; Edmunds & Elahi, 2007; Edmunds, Ross & Didden, 2011), suggesting that habitat fragmentation by bombing has resulted in a permanent localized loss of coral reproductive stock and that in combination with natural low recruitment rates of most reef-building species, natural recovery of composition and functions is very unlikely.

Bombarded areas were also characterized by sustaining lower fish species richness, H'n, abundance, and biomass, as a result of the permanent loss and lack of recovery of reef benthic spatial relief. They also had a very low abundance or absence of significant fish functional groups of herbivores and carnivores, including multiple commercially-important species. These findings are consistent with IDEA (1970) which estimated at least 10 times higher fish densities outside cratered reefs in Culebra Island, though no quantitative parameters were provided. Riegl (2001) found that coral cover decreased, bare substratum and rubble increased, and fish communities changed within areas impacted by blast fishing in Egypt. Depauperate fish assemblages within bombarded reef segments were also consistent with declining fish communities documented on reefs that have already shown rapid benthic community decline as a result of

climate change impacts (Jones, McCormick, Srinivasan & Eagle, 2004, Graham et al., 2006; Pratchett et al., 2008). Such changes may become more pronounced as coral cover continues to decline and as fishing pressure continues to increase (Pratchett, Hoey & Wilson, 2014). Fishing impacts were not a factor in this study as all fish data collection was conducted within the no-take CLPNR. Status of more diverse and rich fish communities across control sites is consistent with previous accounts across similar spatial scales for the site (Hernández-Delgado, Rosado-Matías & Sabat, 2006). Therefore, differences in fish community structure were presumed to occur at the studied spatial scales as the result of altered benthic community structure and spatial heterogeneity due to bombing activities.

Individual reef craters are often small in size (50-400m²) and isolated in space, which render them as very small spatial units generally disregarded as having low ecological significance as they may represent a small geographical proportion of reef surface area in comparison to island wide spatial scales. Studies of bombing impacts at small spatial scales are still very limited. Dodge (1981) found no significant impacts of military bombing on *M. annularis* growth rates on individual coral core samples from Vieques, but Macintyre, Raymond & Stuckenrath (1983) found significant destruction by bombing of shallow *Acropora palmata* (Lamarck, 1816) and *Porites porites* (Pallas, 1766) frameworks. Porter et al. (2011) also found a statistically significant inverse correlation between the coral species richness, colony abundance and species diversity, and the density of military ordnance across reef scales in Vieques. Nonetheless, at smaller ecological scales (e.g., fringing reef unit), reef craters represent localized mosaics of reef segments that were severely reduced to a flattened, unstable, demolished reef bottom, with depauperate biodiversity, that have shown little or no recovery even after three to five decade temporal scales. Placed within the context of current sea surface warming trends, recurrent massive bleaching events, and documented decline

of northeastern Caribbean coral reefs (Miller et al., 2009; Hernández-Pacheco, Hernández-Delgado & Sabat, 2011; Edmunds, 2013), net recovery of ecosystem structure and functions within bombarded grounds is unlikely to occur, rendering them as novel habitats (*sensu* Graham, Cinner, Norström & Nyström, 2014). This suggests that future trajectories of dramatically changed reef communities constituting novel habitats will be quite different from the past, and embracing novel futures may enable more pragmatic approaches (e.g., rehabilitating ecological functions instead of restoring original diversity) to maintaining or re-building the dominance of massive reef-building corals from the past.

The lack of meaningful natural coral reef recovery within 35-50 year-old reef craters from Culebra is alarming, but surprisingly, still poorly addressed. Our study suggests that coral community recovery is minimal within reef craters and limited to sporadic ephemeral species such as *S. radians* and *P. astreoides*. There is increasing evidence that natural coral reef recovery ability from blasting even across small spatial scales can become severely limited with increasing spatial and temporal scale of destruction. Extensively blasted areas for fishing in Indonesia showed no significant recovery within a period of six years despite adequate coral larval supply from adjacent reefs (Fox & Caldwell, 2006). Extensive bombing can result in the formation of unstable coral rubble fields that can move with ocean currents and storm swells, causing extended mortality on adjacent remnant patches of living corals and that can also prevent successful coral larval recruitment over unstable bottoms (Fox, Pet, Dahuri & Caldwell, 2002; 2003; Lindhal, 2003; Raymundo, Maypa, Gomez & Cadiz, 2007). Therefore, reef natural recovery ability within directly bombarded grounds seems poorly probable and will require assisted coral reef rehabilitation methods (Bowden-Kerby, 1997; Raymundo et al., 2007; Hernández-Delgado, Suleimán, Olivo, Fonseca & Lucking, 2011). This can be feasible across small spatial scales similar to those of reef craters. Nonetheless,

human intervention is unlikely to be effective on large spatial scales due to prohibitive costs, highlighting the need for a combination of effective management approaches to foster the rehabilitation of reef ecological functions and ecosystem resilience.

A particular concern is that a habitat once dominated by a *M. annularis* species complex framework has not shown any sign of recovery over the course of several decades through sexual coral larval recruitment. Though coral larval settlement do occur within the crater, coral spat mortality appears to be high largely due to the unstable fragmented nature of the bottom. Considering the significant decline of *M. annularis* species complex percent living cover across the region (Miller et al., 2009; Hernández-Pacheco et al., 2011, Edmunds, 2013), recovering benthic spatial heterogeneity ecological functions is largely improbable. Therefore, an alternative strategy that can potentially achieve rapid results in rehabilitating shallow reef ecological functions as juvenile fish nursery grounds is the use of community-based, low-tech farming and outplanting of rapid-growing *Acropora cervicornis*. Low-tech, community-based approaches to culture, harvest and transplant *A. cervicornis* into formerly bombarded grounds proved highly successful in fomenting increasing benthic spatial heterogeneity, while fostering meaningful community-based participation. Outplanted colonies showed outstanding survival and growth rates. Observed decline occurred as a result of partial coral mortality associated to massive runoff events from deforested steep slopes adjacent to the coastline following heavy rainfall. Higher percent survival rate observed on rocky outcrops at impacted sites (within no-take CLPNR) was the result of lower predation impacts by corallivore gastropod *Coralliophila abbreviata* Lamarck, 1816 and *C. caribaea* Abbott, 1958, and by fireworm *Hermodice carunculata* Pallas, 1766; in comparison to adjacent controls outside the reserve. This could be the result of lack of invertebrate predators across control non-reserve sites, which is consistent with previous accounts of fish community structure

from the site (Hernández-Delgado et al., 2006). This suggests that *A. cervicornis* farming and outplanting is a key successful tool to help rehabilitate shallow reef nursery grounds. But further, it also showed that reef trophic condition is a key element in determining reef rehabilitation success. Therefore, the combination of a no-take marine protected area designation and low-tech coral farming and outplanting are key management tools to foster the rehabilitation of reef ecological functions and ecosystem resilience of impacted sites across reef spatial scales. History has shown that introducing and fostering compliance with coral reef conservation measures in a small island community still traumatized by historical military practices and by past actions by the government perceived by local communities as serious violation of trust has become a paramount challenge. Nonetheless, community-based participatory management approaches have proved to be a highly successful and empowering strategy to rehabilitate impacted coral reefs ecosystems and to educate base communities through hands-on experience on the significance of reef conservation and rehabilitation.

There is also a concern that military impacts on coral reef are ecologically persistent and that they may still represent a risk of toxic pollution further threatening reef recovery. Goenaga (1986, 1991) suggested that the large abundance of unexploded ordnance and the potential leaching of pollutants from bombs in coral reefs may significantly impair their future recreational and fishing value. Porter (2000) found evidence of abundant “unexploded bombs, artillery shells, and shell casings on the coral reef and in adjacent seagrass beds; burial and shading of coral reef organisms by unexploded ordnance and ordnance debris; fracturing of the coral reef framework and the underlying coral bed rock, and the existence of bombs and bomb fragments impregnated into the reef; the existence of parachutes from flares and cluster bomb fragments draped over corals and other coral reef flora and fauna; and the existence of unexploded bombs leaking materials into coral reef environment and

creating a limited “dead zone” around the bombs”. Porter et al. (2011) also found a statistically significant inverse correlation between the density of unexploded ordnance and coral species richness, coral colony abundance, and coral species diversity, with reefs with the highest concentrations of bombs and bomb fragments having the lowest health indices and the lowest species diversity. Further, evidence of leaking toxics from unexploded ordnance has also been documented in reef demersal fauna from Vieques (Porter et al., 2011). These factors, in combination with the long-term impacts of uncontrolled, poorly planned land uses in the post-military land development boom in Culebra and Vieques has also resulted in the implementation of a non-sustainable development model with paramount adverse ecological and socio-economic implications to environmental and socio-economic sustainability of the islands (Hernández-Delgado et al., 2012; Ramos-Scharrón, Amador & Hernández-Delgado, 2012). This is an aspect that deserves further research.

Our findings showed that there was still an untold story about bombing impacts across small reef spatial scales, that benthic habitat destruction is ecologically long-lasting (over decadal scales) and that lack of net recovery has resulted in converting impacted reefs in a *de facto* novel habitat. Natural reef recovery abilities within bombarded reefs need to be continuously monitored. Targeted monitoring efforts will become critical in the context of increasing sea surface temperature and its long-term impacts on coral reefs. Declining reefs across the region due to climate change impacts may aggravate the ability of bombarded reefs to show at least a modest degree of recovery. The lack of natural recovery ability coupled with a declining social-ecological system significantly reduces the probability of ecosystem and socio-economic recovery. A major community-based effort should be launched to foster improved coral reef ecosystem and socio-economic resilience rehabilitation. Integration of local stakeholders should help improve efforts by local natural resource

managers and decision-makers to accelerate recovery of ecological functions of degraded reef ecosystems and socio-economic systems, but also to repair communication and trust.

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RESUMEN

Los arrecifes de coral con craters-bomba en Puerto Rico, la historia no contada sobre un hábitat inusual: desde la destrucción de arrecifes hasta la rehabilitación ecológica basada en la comunidad. Los impactos ecológicos de las actividades militares de bombardeos en Puerto Rico se han descrito a menudo como mínimos, con recurrentes denuncias al confundir efectos por huracanes, enfermedades de corales y estresores antropogénicos locales. Los cráteres de arrecife, aunque aislados, están relacionados con una alta fragmentación de la colonia y pulverización del contorno, con una pérdida neta permanente de arrecife en bio-construcción. En contraste, secciones adyacentes de arrecife no bombardeado tienen mayor biodiversidad y mayor relieve espacial bentónico. Comparamos las comunidades bentónicas en cráteres-bomba de arrecifes de coral con 35-50 años de antigüedad en las islas de Vieques, Puerto Rico, en comparación con los sitios adyacentes no impactados; 2) la densidad de reclutamiento de coral y estructura de la comunidad de peces dentro y fuera de los cráteres; y 3) impactos preliminares de un esfuerzo de rehabilitación basado en la comunidad arrecifal usando tecnología simple con el cultivo del coral *Staghorn Acropora cervicornis*. Los cráteres de arrecife se distancian en tamaño de aproximadamente 50 a 400m² y fueron dominados ampliamente por fragmentos de bentos aplanado, con una cubierta de coral generalmente por debajo de 2% y el predominio de taxones no constructores de arrecifes (es decir, tapetes de algas filamentosas, macroalgas). La

heterogeneidad espacial bentónica fue significativamente menor dentro de cráteres que también resultaron en un reducido valor funcional como tierra de vivero de peces. La riqueza de especies de peces, abundancia y biomasa y densidad coral recluta fueron significativamente menores dentro de cráteres. Tecnología simple, basada en los enfoques de cultivo de comunidad, la cosecha y trasplante de *A. cervicornis* en terrenos anteriormente bombardeados han demostrado un éxito al aumentar el porcentaje de cobertura de coral, la heterogeneidad espacial bentónica y ayudando a rehabilitar funcionalmente la tierra para vivero.

Palabras clave: estructura de la comunidad bentónica, impactos de bombardeo, rehabilitación ecológica basada en la comunidad, arrecifes de coral, estructura de la comunidad de peces, actividades militares, hábitat inusual

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