The mortality, recovery, and community shifts of scleractinian corals in Puerto Rico one decade after the 2005 regional bleaching event

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This work analyzes the mortality, recovery, and shifts in the composition of scleractinian corals in Puerto Rico one decade after the 2005 regional coral bleaching event. Temporal and spatial patterns of coral community structure were examined using a stratified, non-random sampling approach based on five permanent transects per reef at 16 reef stations. A negative correlation between percent coral cover loss and light attenuation coefficient (Kd_{490}) was observed, suggesting that water turbidity played a major role in coral protection during the bleaching event ("sunblock effect"). Loss of coral cover after the bleaching event was lower at nearshore reefs, and with increasing depth at oceanic and shelf-edge reefs. By 2015, coral recovery was observed at all reefs surveyed, but coastal reefs exhibited a higher rate of recovery. The responses of coral assemblages varied after the bleaching event, including shifts in cover from massive corals (*Orbicella* spp.) to turf algae and/or by opportunistic (*Porites astreoides*) and branching corals (*Madracis auretenra*, *P. porites*); partial recovery by *O. annularis* complex; and no measurable change in coral assemblages before and after the event.

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47 **ABSTRACT**

48   This work analyzes the mortality, recovery, and shifts in the composition of scleractinian

49 corals in Puerto Rico one decade after the 2005 regional coral bleaching event. Temporal and

50 spatial patterns of coral community structure were examined using a stratified, non-random

51 sampling approach based on five permanent transects per reef at 16 reef stations. A negative

52 correlation between percent coral cover loss and light attenuation coefficient (Kd_{490}) was

53 observed, suggesting that water turbidity played a major role in coral protection during the

54 bleaching event ("sunblock effect"). Loss of coral cover after the bleaching event was lower at

55 nearshore reefs, and with increasing depth at oceanic and shelf-edge reefs. By 2015, coral

56 recovery was observed at all reefs surveyed, but coastal reefs exhibited a higher rate of recovery.

57 The responses of coral assemblages varied after the bleaching event, including shifts in cover

58 from massive corals (*Orbicella* spp.) to turf algae and/or by opportunistic (*Porites astreoides*)

59 and branching corals (*Madracis auretenra*, *P. porites*); partial recovery by *O. annularis*

60 complex; and no measurable change in coral assemblages before and after the event.

61

62 **INTRODUCTION**

63 Coral reef communities have been changing dramatically over the past four decades (Gardner et

64 al., 2003; Hughes et al., 2003; Jackson et al., 2014). Natural and anthropogenic disturbances

65 have been detrimental to the ecological integrity of coral reefs and the abundance of reef-

66 associated organisms. There have been major declines in large commercially important fish and

67 shellfish, sea urchins and massive corals. Coral bleaching events have been a recurrent

68 phenomenon affecting coral reefs in the Caribbean (Goenaga et al., 1989; Glynn, 1993; Winter et

69 al., 1998; Williams and Williams, 2000; Wilkinson and Souter, 2008; García-Sais et al., 2008),

70 with major events having occurred in 1998 (Winter et al., 1998) and more recently in 2005

71 (García-Sais et al., 2008; Weil, Croquer & Urreiztieta, 2009; Eakin et al., 2010). Long-term data

72 quantifying the impacts of major bleaching events upon reef community structure are lacking in

73 the Caribbean. Specifically, the limited information on long-term responses, including the

74 recovery from large-scale mortality associated with regional bleaching events, is of particular

75 concern.

76   Coral bleaching is the whitening of corals due to the loss of their symbiotic algae.

77 Reductions in salinity (Goreau, 1964; Bahr, Jokiel & Rodgers, 2015), decrease or increase in

78 light (Jokiel, 1980; Lesser, 1996; Lesser et al., 1990; Gleason and Wellington, 1993; Brown,

79 1997; Torres et al., 2007; Torres, Armstrong & Weil, 2008) and an increase in sea surface

80 temperature (Jokiel and Coles, 1977; Jokiel and Coles, 1978; Hoegh-Guldberg and Smith, 1989;

81 Glynn, 1993; Ferrier-Pages et al., 2007) are factors that cause corals to bleach or turn pale. In

82 areas exhibiting higher summer temperatures, higher variability in temperature, and/or a lower

83 rate of seasonal warming, corals are less likely to bleach indicating that a higher rate of

84 adaptation and/or acclimation may make them resistant to bleaching (Castillo and Helmuth,

85 2005; McClanahan et al., 2007; Mumby et al., 2011; Oliver and Palumbi, 2011; Chollett,

86 Enríquez & Mumby, 2014). Several studies have proposed that there is a natural "refugia" with

87 increasing water depth and water turbidity associated with inorganic and organic sources (West

88 and Salm, 2003; Wilkinson and Souter, 2008; Bridge et al., 2013; Smith et al., 2014). In the

89 Indian and Pacific Oceans, the impacts of coral bleaching were less severe in areas of high

90 organic turbidity (van Woesik et al., 2012; Cacciapaglia and van Woesik, 2015).

91   Turbidity can be caused by either inorganic (sedimentation) or organic sources

92 (phytoplankton biomass), each having different environmental implications. Inorganic turbidity

93   is caused by an influx of sediments from coastal development, river runoff, and/or the

94   resuspension of materials in the benthos. The influx of phytoplankton does occur naturally,

95   however, anthropogenic activities influence nutrient loading in coastal environments due to

96   activities including, but not limited to, agriculture and/or sewage leaching. In the west coast of

97   Puerto Rico, a positive correlation has been observed between turbidity and chlorophyll-a

98   (Gilbes, Lopez & Yoshioka, 1996), with western and near coastal coral reefs exhibiting higher

99   levels of chlorophyll-a (Otero and Carbery, 2005). The north and west coasts receive most of the

100   nutrient loading from the discharge of some of the largest rivers (Morelock, Grove & Hernandez,

101   1983), whereas rivers with smaller drainage basins are found along the south coast. There are no

102   rivers in either of the offshore islands (Culebra and Vieques), which are characterized by clear,

103   oligotrophic waters (Morelock, Grove & Hernandez, 1983).

104   The most severe coral bleaching event reported for Puerto Rico and the US Virgin Islands

105   occurred in late August 2005 (García-Sais et al., 2008; Weil, Croquer & Urreiztieta., 2009; Eakin

106   et al., 2010), and coincided spatially and temporally with the passing of a mesoscale anticyclonic

107   eddy across the northern Caribbean (García-Sais et al., 2008). Anticyclonic eddies are recurrent

108   features that occur four to five times a year in the western tropical Atlantic and Caribbean basin

109   (Alvera-Azcárate, Barth & Weisberg, 2009). Given the clockwise circulation and Coriolis

110   forcing, surface waters accumulate at the eddy center causing an increase in the mixed layer

111   depth, therefore limiting heat dissipation and exchange to surrounding water masses (García-Sais

112   et al., 2008). The anticyclone produces a positive anomaly in altimetry. Coral bleaching was

113   severe at many sites throughout the Caribbean during late 2005, affecting 50% to 95% of coral

114   colonies (Wilkinson and Souter, 2008). The effects on Puerto Rican coral reefs were variable

115   between geographic locations, depths, and coral species (García-Sais et al., 2008). More than

116   90% of scleractinian corals displayed signs of thermal stress, becoming pale or bleached

117   (Hernández-Delgado et al., 2006; Miller et al., 2009). *Orbicella annularis* complex was among

118   the most impacted of all coral that bleached in 2005 (García-Sais et al., 2008; Hernández-

119   Pacheco, Hernández-Delgado & Sabat, 2011), with more than 90% of the populations recorded

120   as bleached in Puerto Rico and the U. S. Virgin Islands (Ballantine et al., 2008; Miller et al.,

121   2009).

122   Reports of coral recovery after massive bleaching events in the Caribbean are scarce

123   (Idjadi et al., 2006; Manfrino et al., 2013; Muller, Rogers & van Woesik, 2014). Idjadi et al.

124   (2006) described the phase shift reversal exhibited by Dairy Bull Reef, Jamaica in which live

125   coral cover doubled within a nine-year period (1995 - 2004) up to a maximum cover of 54%

126   largely due to growth of *Acropora cervicornis*. In Little Cayman Island, full recovery of corals

127   was seen seven years after the bleaching event in protected areas (Manfrino et al., 2013). The

128   recovery of corals at Little Cayman Island was attributed to the low anthropogenic disturbance at

129   the reef site. The increase of anthropogenic stressors, such as coastal development,

130   eutrophication and sedimentation, and loss of key reef herbivores have been associated with the

131   lack of coral recovery at many Caribbean coral reefs (Carilli et al., 2009; Wilkinson, 2010; Roff

132   and Mumby, 2012).

133   In this paper we describe the response variability, including the mortality, recovery, and

134   shifts in composition of scleractinian corals on reefs included in the Puerto Rico Coral Reef

135   Monitoring Program (PRCRMP -DNER/NOAA), one decade after the 2005 regional coral

136   bleaching event and analyze the relationships between organic turbidity and coral loss and

137   recovery.

138

139   **MATERIALS AND METHODS**

140   **Study sites**

141   A total of 16 reef stations were included in this time series analysis: Isla Desecheo

142   (hereafter Desecheo), Isla de Mona (hereafter Mona), Rincón, Mayagüez, Cabo Rojo, Guánica,

143   Ponce, and Isla de Vieques (hereafter Vieques). Depth-stratified samplings were performed at

144   Desecheo (15, 20, 30m), Mona (10, 20m), Mayagüez (10, 20, 30m), Rincón (3, 10, 20m), Cabo

145   Rojo (5, 10m), and Vieques (10, 20m). Reef stations in Desecheo, Mona, Mayagüez, and Ponce

146   represent offshore/shelf-edge sites, whereas reefs at Rincón, Guánica, Cabo Rojo and Vieques

147   are representative of coastal sites (Fig. 1). Reef station locations and site names are listed in

148   Table 1.

149

150   **Benthos**

151   At each reef, a set of five permanent 10m long replicate transects were non-randomly

152   established to represent reef areas of optimal coral growth within similar depths (+/- 2m) and

153   reef physiographic zones. Transects were permanently marked with metal rods drilled to the reef

154   substrate at both ends and nails were placed along the length of each transect. Sessile-benthic

155   reef communities were characterized by the continuous intercept chain-link method (as modified

156   from Porter, 1972), following the CARICOMP (1984) protocol. This method provides

157   information on the percent linear cover by sessile-benthic biota and other substrate categories

158   along transects. It allows the construction of reef community profiles by assignment of metric

159   units to each substrate transition, which serves as a high precision baseline for monitoring. The

160   number of chain links per substrate category and species was added and then divided by the total

161   distance (total number of chain links) to calculate the cumulative percent linear cover by each

162   substrate category. The overall mean coefficient of variation of percent live coral cover per reef

163   station (from replicate transects) during the baseline survey was 28% (range: 7.2 - 49.8%).

164

165   **Water quality measurements**

166   Satellite-derived water quality products were used to examine their potential relationship

167   to live coral degradation and/or recuperation. Diffuse attenuation coefficient for downwelling

168   irradiance at 490nm (Kd_{490}) (Mueller 2000, Lee et al. 2005) was used as an index of turbidity

169   and was derived from Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) (O'Reilly et al.,

170   1998; O'Reilly et al., 2000; Maritorena and O'Reilly, 2000,) and Moderate Resolution Imaging

171   Spectroradiometer (MODIS) data. The SeaWiFS and MODIS Aqua satellite Kd_{490} and

172   chlorophyll-a annual data were used from 2000 to 2013 to determine trends in water quality.

173   The study area was 4° x 4°, from 16° to 20^oN latitude and 68° to 64^oW longitude. Level 2

174   satellite products (only available at daily temporal resolution) were selected over Level 3

175   products (available at daily, monthly, and yearly temporal resolutions) since higher spatial

176   resolutions are required for the study of water quality in coastal areas. The spatial resolution of

177   SeaWiFS Level 3 data is 9km and 4km while for MODIS Aqua is 9km. SeaWiFS and MODIS

178   Level 2 data. Selection of coral reef sites' pixel locations was made first by collecting the

179   latitudes and longitudes (lat/lon) as well as depths of each respective site. Representative pixels

180   were then selected in order to avoid the influence of land pixels and pixels influenced by ocean

181   bottom reflectance signal. The lat/lon of the pixels used were selected along a line tangent to the

182   shelf edge and starting at each coral reef site. The lat/lon used was based on where the ocean

183   bottom was not visible while being as close as possible to each coral reef site.

184   SeaDAS v6.4 software was used to perform data visualization (Baith et al., 2001) and to

185   accurately project and ortho-rectifiy the daily Kd_{490} data files into the same Conic Lambert's

186   map projection output. Only data files with minimal or no pixel distortions were selected for the

187   study. Daily Kd_{490} data files picked were re-visualized, using MATLAB version 7.12.0 (The

188   MathWorks Inc., Natick, MA, 2011). This included the transformation of daily data into monthly

189   and annual averages. The reef sites' Kd_{490} values were extracted from their respective lat/lon

190   pixel values using the average annual data files.

191

192   **Statistical analyses**

193   ***Coral cover***

194   Two-way Repeated Measures Analysis of Variance (ANOVA) procedures were run to

195   compare percent reef substrate cover by live scleractinian corals and specifically of percent cover

196   by *Orbicella annularis* complex (hereafter *Orbicella annularis*) between depths and years at

197   each reef. Year and depth were assigned as the within subject factor for the analyses. There were

198   some locations where depth was not a factor (Guánica and Ponce). In those instances, a One-way

199   Repeated Measures ANOVA analysis was used to test variations of percent total coral cover and

200   *Orbicella* spp. cover between years. The assumption of normality was analyzed before running

201   any tests. Coral cover was arcsine transformed before analyses. Bonferroni post-hoc procedures

202   were performed to examine yearly variations of percent coral cover at each site. Repeated

203   measures ANOVA tests were run in SPSS software (version 17.0).

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207   ***Coral assemblages***

208   Two-way distance Permutational Multivariate Analyses of Variance (PERMANOVA)

209   tests (Anderson, 2001) were performed to examine changes in coral assemblages between depths

210   and years at each reef. At reef sites where depth was not a factor, a one-way PERMANOVA

211   analysis was used test the variations in coral assemblages between years. Each PERMANOVA

212   procedure was based on Bray-Curtis similarity measures. Coral species that contributed to more

213   than 10% of the total cover were used for this analysis. *A posteriori* pairwise comparison tests

214   were performed in PERMANOVA to further assess variations within the factors. SIMPER tests

215   were run to identify the contribution of coral species to the overall differences between years.

216   Multidimensional scaling (MDS) plots were produced to examine differences in coral

217   assemblages between years. PERMANOVA, SIMPER, and MDS procedures were performed

218   using PRIMER-e and PERMANOVA add-on software (Anderson, Gorley & Carlke, 2008).

219

220   ***Relationships between change in coral cover and diffuse attenuation coefficient (Kd_{490})***

221   Linear regressions were applied to examine relationships between changes in coral cover

222   at the upper reef depth surveyed (10m depth) and satellite-derived Kd_{490} light attenuation

223   coefficients from the immediate vicinity of reef stations. For changes of coral cover, we

224   calculated the rate of coral cover loss and recovery using 2005 as the baseline, with the exception

225   of Mona where baseline observations were from 2000. The coral cover loss was calculated as the

226   percent difference between 2005 (pre-bleaching) and 2008 at each site. Coral recovery represents

227   the percent increase of substrate cover from 2008 to 2015. Linear regressions were run in SPSS

228   software (version 17.0).

229

230   **RESULTS**

231   **Pre-bleaching event conditions**

232   Oceanic and shelf-edge reefs had the highest percentages of live scleractinian coral cover

233   (hereafter live coral) during the baseline surveys performed before the onset of a regional coral

234   bleaching event in August 2005. Mean live coral cover ranged from 32% to 52% at reef stations

235   from Desecheo (20m and 30m), Mona (20m), Ponce, and Mayagüez (10m and 20m). Coral cover

236   at coastal reefs in Guánica, Cabo Rojo, and Rincón ranged from 10 to 20%, while at coastal reefs

237   at Vieques ranged from 26 to 36% (Fig. 2). Live coral cover increased with depth at Desecheo,

238   but declined with depth at Mayagüez (Fig. 2 e, g).

239   *Orbicella annularis* had the highest percent cover by live corals and the main reef

240   building coral at all reef sites except at Rincón 10m, where *Montastraea cavernosa* was the

241   dominant species. The relative contribution of *O. annularis* to the total coral cover at reefs

242   ranged between 31.4% (Mayagüez 10m) and 79.8 % (Vieques 10m) and largely contributed to

243   the similarity of coral assemblages within reef stations.

244

245   **Post-bleaching event dynamics**

246   An inverse relationship was observed between coral mortality and light attenuation

247   coefficient (Kd_{490}) (Fig. 3a). Offshore and shelf-edge waters were characterized by clear,

248   oligotrophic water, with yearly means of Kd_{490} ranging from 0.018 m^{-1} at Desecheo to 0.024 m^{-1}

249   at Ponce during 2005. Statistically significant declines of live coral cover ranging between 36% -

250   52% were measured during the 2006 annual monitoring survey from oceanic reefs in Desecheo,

251   across all depths surveyed (Fig. 2, Table 2). Significant reductions in coral cover were also

252   measured at Ponce (68%) and Vieques, (33.3% at 10m and 58.6% at 20m). Progressive declines

253   in live coral cover were detected at many of the reef stations until 2008.

254   Minor declines in live coral cover were observed at Mayagüez 10m and 20m (21.0% and

255   25.0%, respectively) and Guánica (38.2%), but differences were not statistically significant

256   (Table 2). Changes in live coral cover were not significantly apparent between pre- and post-

257   bleaching at Mayagüez 30m, reef stations at Rincón (10m and 20m) and Cabo Rojo (5m and

258   10m). In 2005, inshore sites were characterized by low light attenuation, with yearly mean values

259   of Kd_{490} ranging from 0.036 m^{-1} at Mayagüez to 0.056 m^{-1} at Guánica.

260   Depth related variations of coral mortality were evidenced at reefs surveyed off

261   Desecheo, Mayagüez and Vieques. At Desecheo, live coral declined 60% and 62% at 15m and

262   20m, respectively, while the decline at 30m was 43% (Fig. 2g). At Mayagüez, live coral cover

263   declined 21% and 28% at 10m and 20m, respectively, but no measurable difference was

264   observed at 30m. Live coral cover from ref stations in Vieques declined 58.6% at 10m and

265   33.3% at 20m.

266   The 2005 coral bleaching event had a severe impact on the mortality of *O. annularis*.

267   Statistically significant reductions of substrate cover by *O. annularis* were observed at all depths

268   from oceanic island reefs; Desecheo and Mona, the shelf-edge reefs at Ponce, Mayagüez 10m,

269   and the coastal reefs of Vieques (Table 3). The relatively high contribution of *O. annularis* to the

270   total scleractinian coral composition of oceanic and shelf-edge reefs strongly influenced the

271   overall decline of total live coral at these reefs. Conversely, differences in live cover by *O.*

272   *annularis* were not statistically significant at coastal reefs of Cabo Rojo, Rincón, and the deeper

273   sections of the shelf-edge reef at Mayagüez (20m and 30m).

274

Coral recovery

275

276   Recovery trends of coral cover were detected at several reef stations after 2008, however

277   by 2015 live coral cover recovery was measured at all of the long-term reef datasets. A positive

278   correlation between recovery of live coral cover (2008 to 2015) and the Kd_{490} coefficient was

279   observed (Fig. 3b). By 2015, 92.3% recovery from the 22.3% coral loss associated with the

280   bleaching event was measured at Mayagüez 10m. Full recovery (100%) was observed at

281   Mayagüez 20m and recovery has been consistent throughout the years at Mayagüez 30m since

282   2011 (Fig. 2e). In addition, full recovery from pre-bleaching (2005) coral cover was measured at

283   Guánica (101%), and positive increases have been measured at the Rincón reefs (113% and

284   110%). Coral recovery was slower at the shelf-edge and offshore reefs.

285   The magnitude of coral recovery also varied with depth. At Desecheo, highest coral

286   recovery was observed at 15m (71.7%), but moderate recovery was also measured at 20m

287   (37.0%) and 30m (52.7%). By 2015, coral recovery was 57.6% at Ponce. The lack of recent

288   surveys from Cabo Rojo, Mona, and Vieques reef sites limit our assessment of potential recovery

289   at these reef sites.

290

Changes in coral composition

291

292   Marked variations of coral assemblages were observed at reefs severely affected by the

293   2005 coral bleaching event, including those at Desecheo, Mona, Vieques, and Ponce (Table 4,

294   Fig. 4). These reefs were all affected by the sharp decline of cover by *O. annularis*. Variations

295   were dependent on reef geographic location and depth. At Desecheo 15m, the percent live cover

296   of *Porites astreoides* and *Agaricia* spp. was not negatively impacted by the bleaching event and

297   their cover consistently increased through time (Fig. 5b). Despite the partial, yet continued

298   recovery of *O. annularis* during recent years (2013 to present), *P. astreoides* now stands as the

299   main coral species in terms of substrate cover at Desecheo 15m (Fig. 5b). A similar pattern was

300   observed at Desecheo 20m, but the main phase shift of coral dominance was towards *P. porites,*

301   replacing not only *O. annularis* but also *Colpophyllia natans,* which ranked second in cover

302   during the pre-bleaching surveys, yet suffered drastic mortality during 2006 (Fig. 5c). At

303   Desecheo 30m the change in composition was mostly related to the demise of *C. natans,* and the

304   increase in relative abundance of *P. astreoides* and *Agaricia* spp. *O. annularis* was still the

305   dominant coral after the bleaching event.

306   Shifts of the coral assemblage were pronounced at Mona reef stations, where *O.*

307   *annularis* cover decreased to levels below *P. astreoides,* a species that was resilient to the

308   bleaching event (Fig. 5 d, e). *O. annularis* cover at Vieques was also high previous to the

309   bleaching event. There were statistically significant declines in live coral cover by *O. annularis*

310   (Table 4) at Ponce and Vieques reefs, and the loss of coral cover was largely replaced by turf

311   algae. Also, the resilience of other species (*P. astreoides*, *P. porites*, and *Siderastrea siderea*)

312   resulted in changes of coral assemblages.

313   Changes in coral dominance were also evident at Mayagüez 10m (Fig. 5a). The

314   statistically significant decline of cover by *O. annularis* was replaced by branching species, such

315   as *Madracis auretenra* and *P. porites* during a five-year period (2007 - 2011). Since then, a

316   consistent recovery of *O. annularis* has been observed reaching present levels of cover similar to

317   those of *M. auretenra* and higher than those of *P. porites*, which has declined in mean cover at

318   Mayagüez 10m since 2011 (Fig. 5a).

319   Coastal reefs of Cabo Rojo, Rincón, Guánica and deeper stations in Mayagüez (20m and

320   30m) did not exhibit any significant differences in coral assemblages associated with the 2005

321 bleaching event. Moderate declines of substrate cover by *O. annularis* were observed at Guánica

322 and Mayagüez 20 after the bleaching event but since recovered to pre-bleaching conditions.

323

324 **DISCUSSION**

325   Puerto Rican coral reefs have changed significantly during the last decade, both regarding

326 the total live coral cover and relative composition of scleractinian coral assemblages. Localized

327 impacts upon coral reefs associated with anthropogenic activities have been reported (Hughes et

328 al., 2003; Fabricius, 2005; Warne; Webb & Larsen, 2005), but the main driver of change on the

329 Puerto Rican coral reef community has been linked to the 2005 regional coral bleaching event

330 (García-Sais et al., 2008; Bruckner and Hill, 2009). Given the spatial context and long-term data

331 collection of this study, we determined that depth, distance from shore, and reef location relative

332 to riverine discharges were relevant factors influencing the disparity in the resilience of corals in

333 the different reefs to the bleaching event.

334   Elevated sea surface temperature (SST) and time of exposure to the SST anomaly were

335 proposed as the main drivers of the 2005 coral bleaching event (Brown, 1997; Hoegh-Guldberg,

336 1999; Eakin et al., 2010). Fluctuating temperature regimes may allow for greater thermal

337 acclimation at the nearshore environments (Chollett, Enríquez & Mumby, 2014). However, coral

338 reefs surveyed in this study were distributed within the water column surface mixed layer and

339 therefore exposed to similar water temperatures within the 10 - 30 m depth range (Sprintall and

340 Tomczak, 1992; Armstrong, Lopez & Gilbes, 2000; Corredor and Morell, 2001). A distinct and

341 consistent pattern of reduced coral mortality with increasing depth was observed at reefs

342 surveyed from various depths, including those at Desecheo, Mona, Vieques and Mayagüez.

343 Thus, suggesting that light may have played a determinant role as a precursor of coral bleaching

344   and subsequent mortality, perhaps in synergy with elevated SST during the 2005 bleaching

345   event.

346   Light penetration decreases exponentially with depth but is also affected by water

347   turbidity from both inorganic and organic sources. Inorganic suspended sediments can increase

348   turbidity in specific areas affected by riverine inputs. In this study, the main driver of water

349   turbidity variations along the insular shelf and nearby offshore waters around Puerto Rico was

350   chlorophyll-a concentrations, an indicator of phytoplankton biomass (Fig. 6). Due to the

351   oligotrophic conditions of oceanic waters surrounding Puerto Rico, nutrient loadings associated

352   with riverine inputs and other coastal estuarine processes convey for pronounced and distinct

353   neritic-oceanic gradients of water turbidity (Schmuker, 2000; Otero and Carbery, 2005; García-

354   Sais et al., 2008). Contrary to what has been previously observed, oceanic and shelf-edge reefs

355   and reefs located upstream from riverine inputs in this study were the most severely affected by

356   the bleaching phenomena and showed slower recovery of live coral cover compared to their

357   coastal and/or downstream counterparts. For example, Tourmaline reef is located at the shelf

358   edge off Mayagüez Bay and thereby influenced by estuarine conditions and higher water

359   turbidity than the oceanic reefs of Desecheo and Mona on the west coast of Puerto Rico. The

360   marked contrast of live coral loss at the 30 m depths from reef stations at Desecheo 30m (43%)

361   versus Mayagüez 30m (0%), suggests that distance from shore and the inherent increase of water

362   turbidity by phytoplankton towards the coast may have also played a role in coral protection.

363   Likewise, the negligible coral loss observed from the coastal estuarine reefs of the Cabo Rojo

364   and Rincón shelf, influenced as well by estuarine conditions, is in sharp contrast to the

365   significant mortalities observed at similar depths in Vieques, located far from the influence of

366   major rivers. These patterns were supported by the negative relationship measured between coral

367   cover loss and light attenuation ("sunblock effect").

368   Of particular interest and with potentially irreversible consequences for Puerto Rican

369   coral reef community structure is the fact that *Orbicella annularis* (complex), the main reef

370   building coral of Puerto Rican reefs, was severely reduced in live cover by the coral-bleaching

371   event. Drastic declines in *Orbicella* spp. after the 2005 bleaching event were also reported at

372   Navassa Island (Miller et al., 2016). The large-scale degradation of *O. annularis* has implications

373   for structural habitat loss due to bioerosive forces, both in terms of the overall topographic relief

374   and habitat complexity and a loss in overall carbonate production (Edmunds and Elahi, 2007;

375   Alvarez-Filip et al., 2011, Alvarez-Filip et al., 2013; Perry et al., 2013). The susceptibility of *O.*

376   *annularis* to the synergistic effect of elevated water temperature and high levels of ultra-violet

377   radiation is well documented (Goreau and Macfarlane, 1990; Szmant and Grassman, 1990;

378   Castillo and Helmuth, 2005; Manzello et al., 2007; Hernández-Pacheco, Hernández-Delgado &

379   Sabat, 2011; Bayraktarov et al., 2013). Increased protection of live coral cover by *O. annularis*

380   was observed with increasing depth at oceanic and shelf-edge reef sites, as well as at coastal reef

381   stations with higher water turbidity.

382   The variation in the resilience of other coral species after the bleaching event led to

383   changes in coral assemblages at these reef stations. Essentially, four major patterns of coral

384   community structure have been detected since 2005 by this monitoring program; 1) a marked

385   decline of cover by massive corals (*Orbicella* spp.) with a proportional increase in cover by turf

386   algae was evident at offshore stations, 2) a shift in coral assemblage from massive corals to

387   opportunistic coral species (*Porites astreoides*), specifically branching corals (*Madracis*

388   *auretenra*, *P. porites*), 3) a partial recovery by *O. annularis*, which occurred on most reefs

389   surveyed; and 4) no measurable change in coral assemblages before and after the bleaching.

390   Community shifts to opportunistic corals have been previously reported (Green, Edmunds &

391   Carpenter, 2008) and this is due to their inherent life history traits such as short longevity (Soong

392   1991), brooding larvae, and relative high fecundity (Chornesky and Peters, 1987; McGuire,

393   1998). Brooding corals have the capability to survive disturbances (Green, Edmunds &

394   Carpenter, 2008). The shift to weedier coral species can have serious ecological impacts on coral

395   reef function, resulting in the loss of coral calcification and structural complexity (Alvarez-Filip

396   et al., 2013).

397   Due to lingering effects associated with coral disease, most reef sites reached their

398   minimum coral cover by 2008. However, one decade after the bleaching event, coral recovery

399   was observed at all reefs. There have been reports of coral recovery after bleaching events from

400   many parts of the world (Baker et al., 2008; Gilmour et al., 2013; Graham et al., 2013; Manfrino

401   et al., 2013), however this is the second study to report coral recovery in the Caribbean after a

402   major disturbance at a larger scale (multiple reefs). In Puerto Rico, reef decline has been

403   attributed to the increase of sediment discharge and nutrient inputs along the south and west

404   coasts of Puerto Rico (Morelock, Grove & Hernandez, 1983; Warne, Webb & Larsen, 2005).

405   However, we suggest that increased water turbidity by organic sources may have acted as a

406   natural "sunblock" that protected corals from bleaching, and the high plankton biomass affecting

407   water turbidity may have functioned as an available food source for corals to promote faster

408   recovery due to potentially higher growth rates (Wooldridge, 2014). This premise is reinforced

409   by other studies in the Indian and Pacific Oceans (van Woesik et al., 2012; Cacciapaglia and van

410   Woesik, 2015), which observed turbid nearshore environments as climate change refuges with

411   turbidity mitigating high-temperature bleaching. In addition, there have been reports of healthy

412   coral reefs (high coral cover) in the Caribbean in areas of high anthropogenic inputs (García-Sais

413   et al., 2014; López-Victoria et al., 2015).

414   **CONCLUSION**

415   The bleaching event in 2005 was one of the worst disturbance on record for the

416   Caribbean, affecting the coral reef community structure. However, by 2015 coral recovery was

417   observed at all reefs in this study. The bleaching effects were lessened at sites with higher

418   turbidity and in deeper water. This study demonstrates the benefits of organic turbidity

419   ("sunblock effect") in the coral recovery at many inshore reefs in Puerto Rico. Therefore,

420   conservation and management efforts might want to focus on nearshore and/or deep reefs

421   because they may provide refugia for coral populations as bleaching may become a more

422   recurrent event.

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708 **FIGURES**
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710
711   Figure 1. Location of 16 reef stations from eight areas in Puerto Rico: Isla Desecheo, Isla de

712   Mona, Rincón, Mayagüez, Cabo Rojo, Guánica, Ponce, and Isla de Vieques.
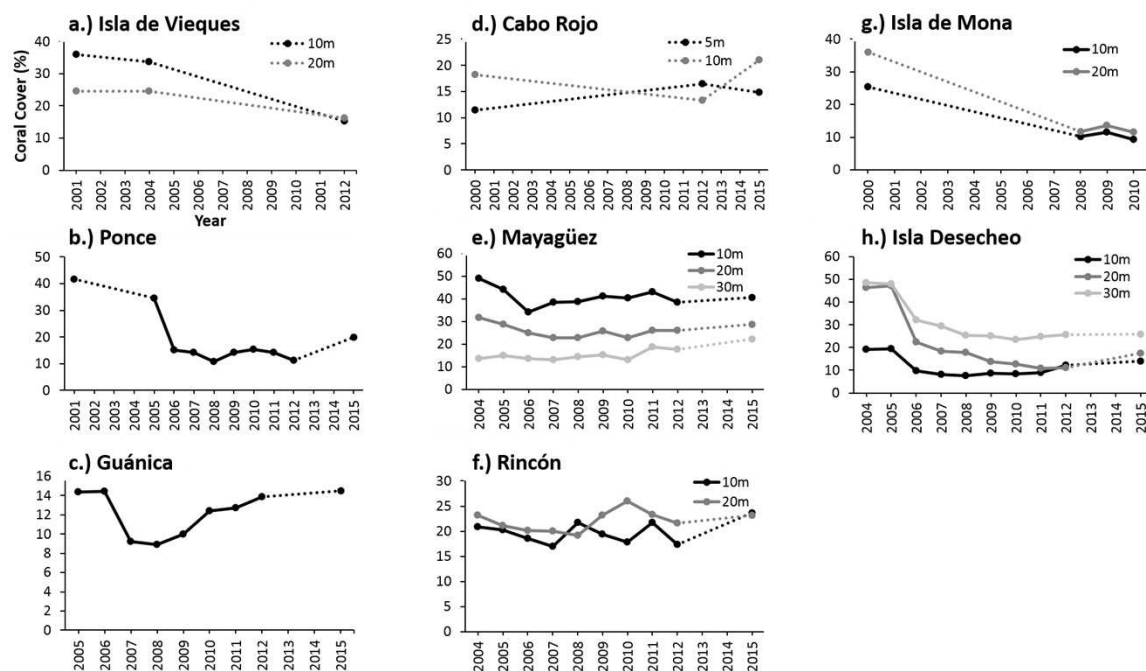
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716   Figure 2. Variations of mean coral cover (%) between monitoring surveys at: a) Isla de Vieques,

717   b) Ponce, c) Guánica, d) Cabo Rojo, e) Mayagüez, f) Rincón, g) Isla de Mona, and h) Isla

718   Desecheo in Puerto Rico. The dashed lines signify years in which no data were collected.

719
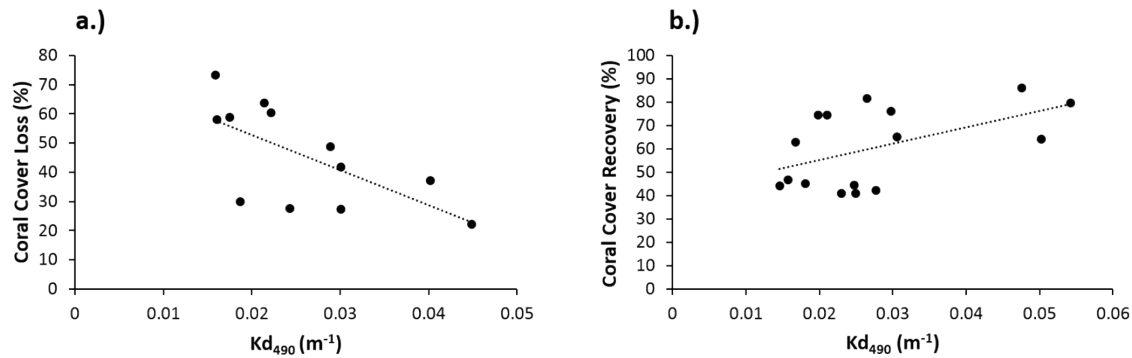720   Figure 3. (a) Negative correlation between coral cover loss (%) and attenuation coefficient

721   (Kd_{490}) during 2006 and 2008 (r^2=0.43, p=0.02) and (b) positive correlation between coral cover

722   recovery (%) and light attenuation coefficient (Kd_{490}) from 2009 and 2012 (r^2=0.39, p=0.02) at

723   reef stations in Guánica, Mayagüez (10m), Ponce, and Isla Desecheo (15m).

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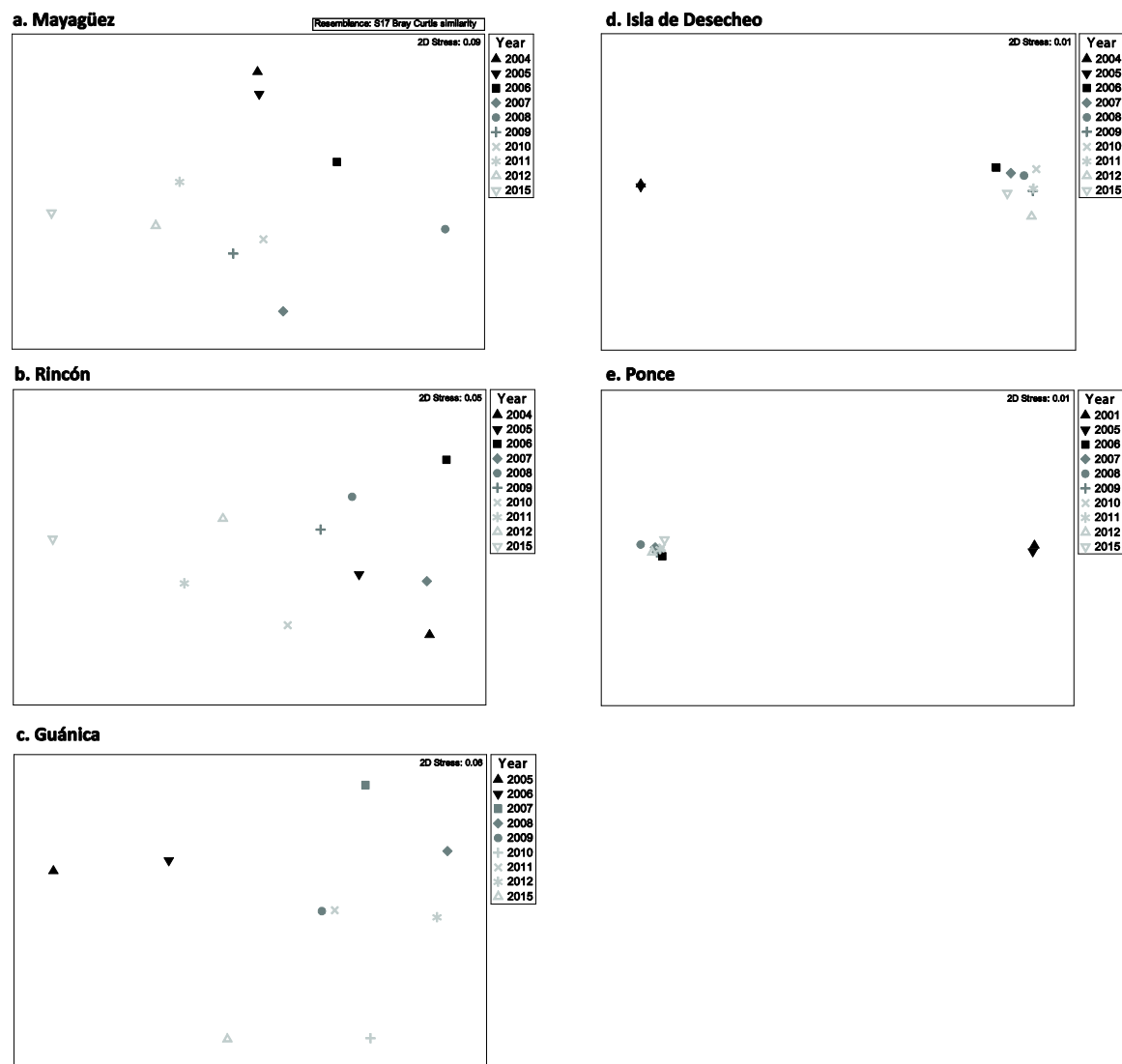
Figure 4. Multidimensional scaling (MDS) plots showing variations in coral assemblages
between monitoring surveys at a) Mayagüez, b) Rincón, c) Guánica, d) Isla Desecheo and e)
Ponce. Given the lack of interaction between year and depth, depths were pooled for
visualization purposes. Due to the low sampling of years, data from Isla de Mona, Isla de
Vieques, and Cabo Rojo were excluded from the MDS. Graphs display distance of centroids with
year as the grouping factor.
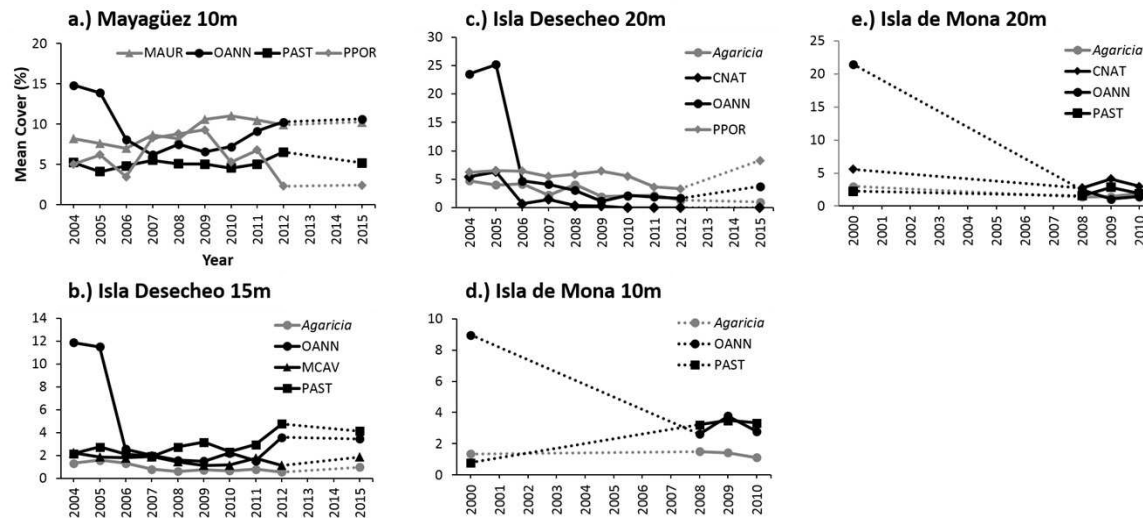
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734 Figure 5. Variations of mean percent cover by coral species during monitoring surveys at: a)

735 Mayagüez 10m, b) Isla Desecheo 15m and c) 20m, and d) Isla de Mona 10m and e) 20m. Coral

736 codes are OANN=*Orbicella annularis* (complex), PAST=*Porites astreoides*, PPOR=*P. Porites*,

737 MAUR=*Madracis auretenra*, and CNAT=*Colpophyllia natans*.

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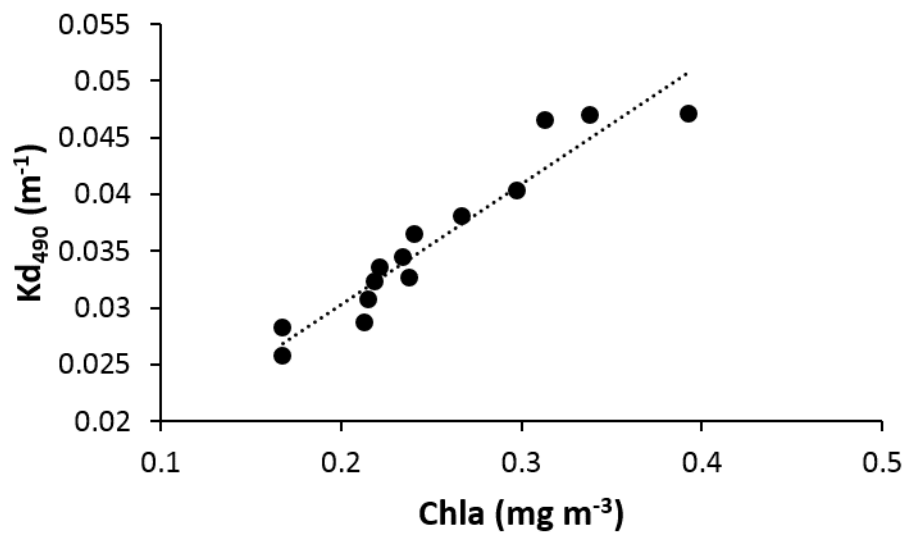
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740　Figure 6. Linear regression showing a positive relationship between chlorophyll-a and

741　attenuation coefficient (Kd_{490}) in the vicinity of reef surveyed in Puerto Rico from 2000

742   **TABLES**
743
744   Table 1. Geographic coordinates, depths and monitoring years for Natural Reserve coral reef
745   sites in Puerto Rico. Abbreviations for reef stations are listed.

Natural Reserve	Sites Names	Latitude	Longitude	Location	Depth (m)	Years
Isla de Vieques	Esperanza	18.298	-65.560	Offshore	10	2001, 2004, 2012
	Canjilones	18.189	-65.698		20	2001, 2004, 2012
Ponce	Derrumbadero	17.904	-66.609	Shelf-edge	20	2005-12, 2015
Guánica	Cayo Coral	17.936	-66.888	Inshore	10	2005-12, 2015
Cabo Rojo	El Palo	18.001	-67.211	Inshore	5	2000, 2012, 2015
	Resuellos	17.991	-67.233		10	2000, 2012, 2015
Mayagüez	Tourmaline	18.166	-67.276	Inshore	10	2004-12, 2015
	Tourmaline	18.165	-67.275		20	2004-12, 2015
	Tourmaline	18.163	-67.274		30	2004-12, 2015
Rincón	Tres Palmas	18.347	-67.270	Inshore	10	2004-12, 2015
	Tres Palmas	18.350	-67.266		20	2004-12, 2015
Isla Desecheo	Puerto Botes	18.382	-67.488	Offshore	15	2004-12, 2015
	Puerto Botes	18.382	-67.489		20	2004-12, 2015
	Puerto Canoas	18.378	-67.487		30	2004-12, 2015
Isla de Mona	Las Carmelitas	18.099	-67.938	Offshore	10	2000, 2008-10
	Playa Mujeres	18.072	-67.937		20	2000, 2008-10

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767 Table 2. Results of two-way and one-way repeated measures ANOVA procedures testing the
768 variations of coral cover between depths and year at the different natural reserve reef sites in
769 Puerto Rico.

Site	Factor	Type III SS	df	MS	F	p value
Vieques	Depth	0.029	1	0.029	4.178	0.110
	Year	0.203	2	0.101	6.959	0.018
	Depth*Year	0.033	2	0.017	1.779	0.229
Ponce	Year	1.622	9	0.18	20.13	<0.0001
Guánica	Year	0.320	8	0.140	2.200	0.050
Cabo Rojo	Depth	0.076	1	0.076	23.751	0.008
	Year	0.039	2	0.020	2.880	0.114
	Depth*Year	0.024	2	0.012	1.353	0.312
Mayagüez	Depth	1.885	2	0.942	10.591	0.006
	Year	0.102	9	0.011	1.976	0.072
	Depth*Year	0.076	18	0.004	0.611	0.879
Rincón	Depth	0.013	1	0.013	0.966	0.381
	Year	0.023	9	0.003	1.033	0.434
	Depth*Year	0.020	9	0.002	2.283	0.038
Desecheo	Depth	1.510	2	0.755	26.325	<0.0001
	Year	1.021	9	0.113	17.620	<0.0001
	Depth*Year	0.624	18	0.035	4.746	<0.0001
Mona	Depth	0.018	1	0.018	1.404	0.302
	Year	0.307	3	0.102	55.656	<0.0001
	Depth*Year	0.017	3	0.006	0.887	0.476

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790 Table 3. Two-way and one-way repeated measures ANOVA procedures testing the variations of
791 reef substrate cover by *Orbicella annularis* (complex) between depths and year at the different
792 natural reserve sites surveyed in Puerto Rico.

Site	Factor	Type III SS	df	MS	F	p value
Vieques	Depth	0.068	1	0.068	3.357	0.141
	Year	0.166	2	0.082	9.646	0.007
	Depth*Year	0.006	2	0.003	0.738	0.508
Ponce	Year	0.217	9	0.024	19.204	<0.0001
Guánica	Year	0.008	8	0.001	1.616	0.159
Cabo Rojo	Depth	0.001	1	0.001	0.362	0.58
	Year	0.006	2	0.003	2.114	0.183
	Depth*Year	0.007	2	0.003	1.591	0.262
Mayagüez	Depth	0.458	2	0.229	16.585	0.001
	Year	0.047	9	0.005	10.36	<0.0001
	Depth*Year	0.029	18	0.002	2.338	0.006
Rincón	Depth	0.136	1	0.136	5.074	0.087
	Year	0.004	9	0	1.081	0.4
	Depth*Year	0.006	9	0.001	1.274	0.284
Desecheo	Depth	0.592	2	0.296	20.384	0.001
	Year	0.657	9	0.73	12.233	<0.0001
	Depth*Year	0.077	18	0.004	2.454	0.123
Mona	Depth	0.004	1	0.004	0.97	0.38
	Year	0.126	3	0.042	10.781	0.001
	Depth*Year	0.038	3	0.013	9.084	0.002

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813 Table 4. Permutational Multivariate Analysis of Variance (PERMANOVA) procedures testing
814 the variations of coral composition between years and depths.

Site	Factor	SS	df	MS	Pseudo-F	p value
Vieques	Depth	2127.6	1	2127.6	2.047	0.089
	Year	8344.9	2	4172.5	4.014	0.002
	Depth*Year	3983.3	2	1991.6	1.916	0.051
Ponce	Year	20331	9	2259	3.156	0.001
Guánica	Year	9189.11	8	1148.6	0.649	0.967
Cabo Rojo	Depth	2246.6	1	2246.6	1.665	0.163
	Year	4576.1	2	2288	1.696	0.11
	Depth*Year	3679.9	2	57010	1.364	0.24
Mayagüez	Depth	1.14E+05	2	866.61	65.686	0.001
	Year	7799.5	9	600.99	0.999	0.453
	Depth*Year	10818	18	867.92	0.692	0.98
Rincón	Depth	7940.8	9	882.32	0.623	0.975
	Year	46299	1	46299	32.667	0.001
	Depth*Year	4514.5	9	501.61	0.354	1
Desecheo	Depth	87185	2	43593	29.496	0.001
	Year	35250	9	3916.7	2.65	0.001
	Depth*Year	25523	18	1418	0.959	0.612
Mona	Depth	6247.1	1	6247.1	3.416	0.007
	Year	14760	3	4920	2.69	0.004
	Depth*Year	5582.1	3	1860.7	1.102	0.449

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