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## Change detection in a Marine Protected Area (MPA) over three decades on Bonaire, Dutch Caribbean

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1 **Change detection in a Marine Protected Area (MPA) over three decades on Bonaire, Dutch**  
2 **Caribbean**

3  
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26 ***Abstract***

27

28 The island of Bonaire is a long-established Marine Protected Area (MPA), the reefs of which  
29 were extensively mapped in the early 1980s. Satellite remote sensing techniques were used to  
30 construct reef maps for 2008-09. Metrics describing the spatial structure of coral habitat at the  
31 landscape scale - including coral cover, fragmentation, patch size and connectivity between  
32 patches - were calculated and compared between these two time periods. Changes were  
33 evaluated in and out of the MPAs and in areas exposed and sheltered from storm damage.  
34 Overall, coral cover has declined during the past three decades, being replaced by sand, but the  
35 decline has not been as drastic as elsewhere in the Caribbean. Fragmentation of the reef habitat  
36 has occurred, resulting in smaller and more disparate patches, but these changes were not  
37 associated with exposure along the coastline. However, total coral cover was maintained in  
38 sheltered areas, whereas it declined along exposed shorelines. Human protection of reefs by  
39 marine reserves had variable effects on coral cover and fragmentation. One of two no-diving  
40 marine reserves showed increases in coral cover accompanied by decreases in the number of  
41 patches of coral and an increase in the size of individual patches over the time period, while the  
42 second reserve exhibited the opposite trend. Advances in satellite remote sensing techniques  
43 allow for a more rapid assessment of changes in reefs at the landscape level, which can be used  
44 to identify spatial changes in the reef environment, including areas of coral decline.

45

46 **Keywords** Marine Protected Area (MPA), coral reef, landscape ecology, fragmentation,  
47 remote sensing

48

## 49 INTRODUCTION

50

51           Understanding the spatial distribution of species and habitats at multiple spatial scales is  
52 of central importance to ecology (He & Legendre, 2002; Harte et al., 2005). Patterns in the  
53 distributions of species and habitats across space provide information critical to our ability to  
54 interpret the forces that structure and maintain ecological diversity (Gaston & Blackburn, 2000),  
55 particularly over time (Gardner et al., 2003). There is evidence that the spatial integrity of key  
56 habitats at the landscape scale is important for the continued success of conservation areas in a  
57 changing world (Saunders et al., 1991; Opdam & Wascher, 2004), with both habitat loss and  
58 habitat fragmentation being of concern. Fragmentation is more than just the loss of habitat, but  
59 loss such that small, isolated patches are created, changing the properties of the remaining habitat  
60 (van den Berg et al., 2001). In coral reef environments, many studies have investigated temporal  
61 changes in fine-scale patterns in reef structure (e.g. Bak et al., 2005) or regional patterns  
62 (Gardner et al., 2003), but few have investigated mesoscale change, at the scale of landscapes  
63 (~100s of m to 10s of km; Turner et al., 2003). It is crucial, as we are experiencing worldwide  
64 declines in coral reef habitats, to understand how local, regional, and global impacts combine to  
65 affect the reef's structure.

66           The island of Bonaire, Dutch Caribbean, represents a unique, long-established Marine  
67 Protected Area (MPA). The Bonaire Marine Park (BMP) was established in 1979, after a series  
68 of other marine conservation measures, including increasing protection for turtles (1961),  
69 prohibitions on spear fishing (1971) and protection for corals, living or dead, from removal,  
70 damage by anchor dropping, and contact from divers (1975). In 1991 two marine reserves were  
71 simultaneously established that excluded underwater visitors, and the BMP was given full

72 protection out to the 60 m depth contour. In 1999, the BMP gained national status as a park of  
73 the Netherlands Antilles and became the Bonaire National Marine Park (BNMP), owing, at least  
74 in part, to the long-term protection they have received, the reefs of Bonaire are thought to be  
75 amongst the most 'pristine' coral reef environments in the Caribbean (Stokes et al., 2010).

76 In 1985, Dr. Fleur van Duyl published the *Atlas of the Living Reefs of Curaçao and*  
77 *Bonaire (Netherlands Antilles)*, comprehensively mapping the coral reefs off the leeward coasts  
78 of Bonaire and Curaçao, an island to the west of Bonaire (Figure 1). The map classified the  
79 subtidal substratum into dominant benthic community types out to 10 m depth based on data  
80 collected by low-altitude aerial photography and ground truthed extensively by scuba diving in  
81 the early 1980s. Van Duyl (1985) found coral to be the dominant bottom-type, making up around  
82 62% of the benthos off the leeward side of Bonaire in shallow water (< 10 m). The total amount  
83 of coral cover was made up of nearly 40% *Acropora cervicornis* and 40% head coral, with the  
84 most common head corals being *Montastraea annularis*, *M. cavernosa*, *Diploria strigosa*,  
85 *Siderastrea siderea*, *S. radians*, *Dichocoenia stokesii*, *Colpophyllia natans*, *Porites astreoides*,  
86 *Meandrina meandrites*, and *Stephanocoenia intersepta*. Head corals in this group were  
87 sometimes accompanied by the foliate *Agaricia* spp. and finger corals were often present in this  
88 group (van Duyl, 1985). Since van Duyl's work was completed, cover of *A. cervicornis* has  
89 dropped to nearly zero, but increases in the head coral group have occurred at various locations  
90 along the coast (Relles & Patterson, *unpublished*).

91 Satellite remote sensing has proven to be an effective technique for creating benthic  
92 habitat maps in coral ecosystems at coarse habitat resolution (3-4 bottom-type classes) and less  
93 than 20 m deep (Mumby et al., 1997; Mumby et al., 1998; Mishra et al., 2006; Relles et al.  
94 2012). Temporal change detection techniques (Jensen, 2005) can then be employed to compare

95 changes in coral cover, or other substrata of interest, on a pixel-by-pixel basis, while computing  
96 total changes at the landscape level. The advantage of satellite remote sensing combined with  
97 change detection techniques is that total loss versus fragmentation can be rapidly quantified.  
98 Because fragmentation is a landscape-level process, fragmentation measurements are correctly  
99 made at the landscape scale (McGarigal et al., 2002,; Fahrig, 2003), but this has rarely been done  
100 on coral reef habitats. Decreases in patch size and increases in the isolation of patches lead to  
101 reductions in population connectivity and are of particular concern for small reef-dwelling  
102 organisms with limited adult ranges and could potentially affect reproduction or dispersal  
103 (Schroeder, 1987). Coral reefs, like most habitats, offer a number of advantages to their  
104 denizens, including protection from predation and a location to forage and find mates. The  
105 complex structure of coral reefs provides the physical habitats and shelter sites that  
106 accommodate many size classes of associated organisms. The ability to make landscape-level  
107 maps of coral cover is important for conservation efforts and of particular interest to government  
108 officials and Marine Protected Area (MPA) managers. Coastal habitat maps are a fundamental  
109 requirement in establishing coastal management plans for systems like coral reefs (Cendrero,  
110 1989; Relles et al., 2012).

111 In this study, a recent (2008-09) satellite-derived map of the reefs of Bonaire (Relles et  
112 al., 2012) is compared to the habitat maps (van Duyl, 1985) from data collected in the early  
113 1980s to identify areas of coral habitat loss and reef fragmentation. The changes in the spatial  
114 structure of these coral habitats between the two time intervals are described at the landscape  
115 scale using metrics of cover of coral and sand cover, fragmentation, patch size and connectivity  
116 between patches. These changes were evaluated in areas within the no-diving marine reserves  
117 and comparably sized unprotected sites to determine whether the lack of underwater visitors has

118 had a significant positive impact on coral cover. The changes in reef structure associated with  
119 broad-scale disturbance from storms are also assessed by comparing areas exposed to and  
120 sheltered from predominant tropical cyclone tracks. This study complements previous research  
121 conducted at a finer-scale, from line transects and quadrats (Bak et al., 2005; Steneck et al.,  
122 2011).

123

## 124 MATERIALS AND METHODS

125

### 126 Baseline data

127

128 The island of Bonaire is located in the southern Caribbean Sea, approximately 80 km off  
129 the coast of Venezuela (12°10' N 68°17' W; Figure 1). This study focuses on the reefs off the  
130 leeward coast of Bonaire, including the accompanying uninhabited island to the west, Klein  
131 Bonaire (Figure 2). Maps of dominant coral community type and other bottom-types (e.g. sand,  
132 rubble, shore zone, and marine plants) were mapped in the early 1980s using aerial photographs  
133 and scuba diving to a depth of 10 m (van Duyl, 1985). As an ancillary data source there is  
134 significant potential for error in the van Duyl (1985) dataset. The maps were created from aerial  
135 photographs taken from variable altitude and the scale of the photographs fluctuated. The maps  
136 were then constructed using the most recent base maps available at the time, which were from  
137 1963 (van Duyl, 1985). The atlas was digitized into images (TIFF format) and subsequently  
138 georectified using ArcGIS 9.3 (ESRI). To align the maps with the coast on the satellite images,  
139 between 12 and 18 control points were identified using the georeferencing tool in ArcGIS, which  
140 allowed features identified by van Duyl (1985) to be aligned to the satellite images (e.g. distinct

141 terrestrial features of coastal morphology, piers and other permanent structures). Based on the  
142 control points, ArcGIS was used to compute spatial residual error values, a measure of the fit  
143 between the true location on the image itself and the transformed locations of the output control  
144 points. Control points with the highest levels of error were then removed until the total root mean  
145 square error (RMSE), a statistical measure of the magnitude of variability between the shape of  
146 the original file and the shape of the georectified file, was less than 9, without dropping the total  
147 number of control points below six. The resulting benthic habitat maps were saved as raster files.  
148 Van Duyl's (1985) 30 maps of Bonaire's leeward reefs varied with respect to the presence of  
149 distinctive features to identify along the present coastline in the satellite images and therefore in  
150 the number of useful control points and this is a potential source of error in the resulting raster  
151 datasets. Polygon vector shapefiles were drawn manually around each of van Duyl's original  
152 bottom-types using the editor function of ArcGIS 9.3 (ESRI). After creation of these polygons  
153 based on the van Duyl (1985) maps, bottom-types were reclassified into the coarser class  
154 distinctions of coral, sand, and sand/coral to match the discrimination capabilities of the satellite  
155 remote sensing techniques (Table 1). The polygons were then converted to raster files at a  
156 resolution comparable to the satellite imagery. While van Duyl mapped areas of coral with  
157 percent cover ranging from 10-20, 20-40, and > 40%, satellite data were coarsely classified as  
158 coral if they contained greater than 20% coral cover. For this reason, areas considered to be 10-  
159 20% coral by van Duyl's classification were included in the sand/coral mixture class.

160

161 **Satellite-derived data groundtruthed from scuba surveys and CPCe**

162



163 Three multi-spectral, high-resolution (2.4 m pixel) images from the QuickBird (QB)  
164 satellite acquired in 2008 and 2009 along the leeward coast of the island of Bonaire, including  
165 the small, uninhabited neighboring island of Klein Bonaire, were prepared and analyzed to create  
166 benthic habitat maps. This required a first-order atmospheric correction, which removed the  
167 scattering effects of light and other electromagnetic radiation by particles smaller than the  
168 wavelength of light (Rayleigh scattering) and the scattering of radiative energy by processes at  
169 the aerosol and molecular level, particles larger than the wavelength of light. The effects of  
170 variable depth were accounted for using the model derived by Lyzenga (1978 & 1981; Mumby et  
171 al., 1997; Mishra et al., 2006) in order to remove water column attenuation effects. Tidal stage at  
172 the time of acquisition of the satellite images was insignificant; Bonaire has a micro-tidal range,  
173 with a mean tidal range of around 10 cm (Kjerfve, 1981). As a result, any tidal variation between  
174 datasets used in this study were within our observational measurement error. Estimating the  
175 bathymetry allowed the effects of particulates and chlorophyll in the water, as well as bottom  
176 albedo, to be removed from the imagery (detailed in Relles et al., 2012). After these corrections,  
177 an image of the remote sensing reflectance from the bottom comprised of three bands (red, blue  
178 and green) was analyzed using the computer program ERDAS® Imagine. The Iterative Self  
179 Organizing Data (ISODATA) algorithm was used to perform an unsupervised classification of  
180 the benthos into 10 classes based on the optical properties of the pixel (Jensen, 2005; Mishra et  
181 al., 2006). Those classes were then named and grouped together based on the dominant benthos  
182 found in each, which was ascertained by visual scuba surveys collected in January 2008.  
183 Seventeen underwater video transects were collected along the leeward coast out to a depth of 20  
184 m and analyzed as individual screenshots using the program Coral Point Count with Excel®  
185 Extensions (CPCe; Kohler & Gill, 2006). These groupings resulted in three coarse classes: sand,

186 coral, and a sand/coral mixture (Relles et al., 2012), which were then used to perform a  
187 supervised classification of the benthos. QB imagery has proven useful for such coarse  
188 classifications (3-4 classes) in coral reef habitats (Mishra et al., 2006). Details on the algorithms  
189 for atmospheric and water column corrections, as well as the classification system, are described  
190 extensively in Relles et al. (2012). The coral class included areas where live hard coral cover was  
191 greater than 20%, while the sand class had greater than 50% sand cover, generally the rest of the  
192 area was covered in the exposed calcium carbonate skeleton. The sand/coral mixture class  
193 contained some mixture of less than 20% hard coral and less than 50% sand with the additional  
194 cover attributed to the presence of octocorals, various marine plants, including *Sargassum* spp.,  
195 or dead coral with algae based on video collected by scuba.

196         Several types of metrics can determine the accuracy of a classification; overall accuracy  
197 is simply the sum of correctly labeled test sites divided by the total number of test sites, while  
198 user accuracy is the probability that a classified pixel actually represents that category on the  
199 ground (Mumby et al., 1997). The overall accuracy of the classification system used here was  
200 71%, with a user accuracy for the sand class of 94% and a user accuracy for the coral class of  
201 50%. The lower level of user accuracy for the coral class is a potential source of error in the  
202 classification system for the satellite-derived 2008-09 data set and could potentially result in a  
203 coral pixel being mislabeled as sand. Using this system a total of 6.8 km<sup>2</sup> of reef along more than  
204 50 km of leeward coastline was mapped out to a depth of approximately 10 m.

205

## 206 **Harmonization of data**

207

208 Prior to comparison of the two data sets (i.e., 1980s and 2008-09), it was necessary to  
209 adjust the spatial resolution such that both data sets had the same resolution as the lowest  
210 resolution data set; in this case van Duyl (1985). The minimum mapping unit (MMU), which  
211 represents the minimum size of a polygon delineated by van Duyl (1985), and presumably the  
212 smallest habitat area discernible in the aerial photographs used to create the maps, was 9 m x 9 m  
213 (81 m<sup>2</sup>). The classified 2008-09 satellite images were then down-resolved from their original 2.4  
214 m x 2.4 m pixels (5.76 m<sup>2</sup>) by resampling the 2.4 m pixels into 9.6 m pixels using a majority  
215 rule. This resampling is a potential source of error as the 2.4 m pixels in the satellite data set  
216 were down-resolved to 9.6 m, the majority rule of resampling potentially causes a pixel that is  
217 coral to change to sand if the majority of pixels in the resampling area are sand. The same is true  
218 for a sand pixel surrounded by coral, but the down-resolving is necessary for change detection  
219 comparisons between the two data sets.

220

### 221 **Change detection**

222

223 The categories of coral, sand/coral, and sand were represented numerically as 1, 2, and 3,  
224 respectively in the van Duyl data set, hereafter referred to as 1980s; and 10, 20 and 30,  
225 respectively, for the satellite data set, hereafter referred to as 2008-09. Because of this coding  
226 convention, progression from the ones column to the tens column of the resulting sum would  
227 represent the change in bottom-type from 1980s to 2008-09 (Table 2). Changes were quantified  
228 as positive, negative, or neutral/no change. Change was considered positive when a pixel that  
229 was something other than coral changed to coral. It was also considered positive when an area  
230 previously dominated by sand became an area of sand/coral mixture. Negative changes occurred

231 when coral changed to anything that was not coral, including when an area of sand/coral mixture  
232 changed to exclusively sand.

233

#### 234 **Patch dynamics**

235

236 Raster data for both years were analyzed using FragStats 3.3 (McGarigal et al., 2002),  
237 which calculated patch, class, and landscape metrics. A patch is defined as an area of similarly-  
238 classified pixels, using an eight-cell rule that takes into consideration all eight adjacent cells,  
239 including the four orthogonal and four diagonal neighbors, to determine patch membership. The  
240 classes in this case were coral, sand, and sand/coral mixture, as described above. In addition to  
241 calculating the number and size of patches, including total patch area and perimeter-to-area ratios  
242 (PARA), two indices of connectivity between patches were also calculated: a contiguity index  
243 (CONTIG) and the Euclidean Nearest Neighbor (ENN) distance. Contiguity is quantified in  
244 FragStats by convolving a 3 x 3 pixel template with a binary digital image in which the pixels  
245 within the patch of interest are assigned a value of 1 and the background pixels (all other patch  
246 types) are given a value of zero. Template values of 2 and 1 are assigned such that orthogonally  
247 contiguous pixels are weighted more heavily than diagonally contiguous pixels; the contiguity  
248 value for a pixel is the sum of the products of each template value and the corresponding input  
249 image pixel value within the nine cell neighborhood. Contiguity values range between zero and  
250 one, with large contiguous patches resulting in larger values, as opposed to smaller, more  
251 disparate patches (McGarigal et al., 2002). The isolation of patches of coral was measured using  
252 the ENN approach, the shortest straight-line distance between the focal patch and its nearest  
253 neighbor of the same class (McGarigal et al., 2002), which hereafter will be referred to

254 connectivity of the reef habitat. Patch, class, and landscape metrics for the two data sets, 1980s  
255 and 2008-09, were compared statistically using an ANOVA when the data was normally  
256 distributed and the Mann-Whitney Rank Sum Test and Kruskal-Wallis nonparametric test when  
257 the data was not normally distributed.

258

### 259 **No-diving marine reserves**

260

261         The farthest northwest marine reserve closed to divers was designated marine reserve  
262 number one (MR1) and was considered an exposed site because its position along the coastline  
263 left it potentially more exposed to storms. A comparable site of equal size and adjacent to MR1  
264 was identified as nMR1 and considered to be an exposed site in a similar area along the coast  
265 that was not closed to divers and other underwater visitors. The second marine reserve is located  
266 farther south along the coast and is sheltered by the northwestern portion of the island and was  
267 designated MR2. A comparable site of equal size to the east of MR2 was designated as the non-  
268 reserve, sheltered site, nMR2. MR1, nMR1, MR2 and nMR2 are shown in Figure 2B. These four  
269 sites were compared to look at the patch statistics described above and compare marine reserve  
270 to non-reserve, exposed versus sheltered sites, and the earlier, 1980s data to the 2008-09 satellite  
271 data. The Mann-Whitney Rank Sum Test was used to determine which year, exposure, and  
272 marine reserve status combinations were significantly different from one another in terms of  
273 connectivity; because there were 21 pairwise comparisons of the seven combinations (only one  
274 patch in MR1 in the early 1980s, therefore no ENN value) the alpha level of significance was  
275 adjusted accordingly by dividing it, 0.05, by 21, resulting in an  $\alpha$  of 0.0024 (Bonferroni  
276 adjustment).

277

278 **Klein Bonaire coastline exposure**

279

280 The small island of Klein Bonaire, located just west of the main island of Bonaire, is  
281 uninhabited. The western portion of the island is exposed to incoming waves and storm energy,  
282 while the eastern portion is sheltered by the main island. The island was divided into exposed  
283 and sheltered (Figure 2C) and the two halves were statistically analyzed to compare the patch  
284 statistics described above for the exposed vs. sheltered halves between the 1980s and 2008-09.

285

286 **RESULTS**

287

288 **Baseline reef environment**

289

290 In the early 1980s, 707 hectares of reef offshore of the leeward coast of Bonaire was  
291 mapped (van Duyl, 1985). Sixty-two percent of this area represented greater than 20% hard coral  
292 cover at the time (441 ha), while areas of high sand cover ( > 50% sand) made up almost 32%  
293 (226 ha). The remaining 6% was composed of a sand/coral mixture (40 ha), which included soft  
294 corals, as well as dead coral covered with algae, and other marine plants.

295

296 **Current reef environment**

297

298 In 2008-09, 695 hectares of the 707 hectares of reef that were mapped in the early 1980s  
299 were remapped using satellite remote sensing techniques; the disparity in area mapped was a

300 result of cloud cover in the satellite images. Slightly greater than 30% of the 92.2 m<sup>2</sup> pixels  
301 represented areas of greater than 20% hard coral cover (210 ha). Sandy bottom (>50% cover)  
302 dominated 53% of the reef, approximately 370 ha, while the remaining 17% of the reef (115 ha)  
303 was covered by a sand/coral mixture, often accompanied by octocorals (e.g. sea whips and  
304 gorgonians), dead coral covered with algae, and marine plants.

305

### 306 **Changes in the reef environment**

307

308         Considering the leeward coast in its entirety, areas of no change made up 45% of the total  
309 reef area and negative change occurred on 43% of the total area, while areas of positive change  
310 were only found in 12%. For areas previously dominated by coral, 47% became sand, while 36%  
311 stayed coral. The largest percentage of sand pixels from the 1980s data set remained sand in  
312 2008-09 (66%), while 18% became coral and 15% changed to a sand/coral mixture. The largest  
313 percentage of the sand/coral mixture pixels changed to sand in 2008-09 (43%), 24% remained  
314 sand/coral, while 34% changed to coral.

315         The northwest coast, most of which is uninhabited because it includes Washington  
316 Slagbaai National Park (Figure 2a), experienced the highest area of negative change (51%), with  
317 60% of coral pixels changing to the sand/coral mixture class or to just sand. While 82% of the  
318 area was represented by coral in the 1980s (133 ha), coral dropped to 38% of the area in 2008-09  
319 (61 ha; 3A.), and the area of sand increased from 16% (26 ha) to 55% (89 ha; Figure 3C). The  
320 sand/coral mixture class experienced an increase from 2% (3 ha) to 7% (11 ha) from the early  
321 1980s to 2008-09 (Figure 3B).

322 The coast of the central part of the island (Figure 2b), which includes one of the no-  
323 diving marine reserves (MR2) and the capital city (Kralendijk), extends 16 km along the  
324 coastline to the north of the city, experienced the highest level of positive change (33%) and the  
325 lowest level of negative change (26%) of the four areas. A larger portion of this coastal area was  
326 coral in the early 1980s (64%) than in 2008-09 (52%; Figure 3A). The sand/coral mixture  
327 increased from 8% in the early 1980s to 29% in 2008-09 (Figure 3B). Correspondingly, the  
328 amount of sand cover in the area declined from 28% to 19% (Figure 3C).

329 The southern coast is also sparsely inhabited and consists mostly of salt pans for the  
330 island's sea salt industry (Figure 2c). In the early 1980s, 55% of this portion of the coastline was  
331 covered in coral (158 ha), which dropped to 19% in 2008-09 (52 ha; Figure 3A).  
332 Correspondingly, sand cover increased from 38% (109ha) to nearly 70% (190 ha; Figure 3C).

333 The uninhabited island of Klein Bonaire, located approximately 1 km west of Bonaire,  
334 experienced declines in coral cover from 52% (59 ha) to 20% (23 ha) over the time period  
335 (Figure 3A). Thirty-four percent of the coral pixels changed to sand, while 35% changed to the  
336 sand/coral mixture, resulting in an increase in the sand/coral mixture class from 3% (4 ha) to  
337 24% (27 ha; Figure 3B), and the sand class from 45% (51 ha) to 56% (63 ha; Figure 3C).

338

### 339 **Whole island patch dynamics**

340

341 While the total percentage of area covered by coral declined from 62% in the 1980s to  
342 30% in 2008-09 (Figure 3A), the number of patches of coral increased from 72 to 221 (Figure 4).  
343 Mean patch size decreased from 6.12 ha to 0.95 ha ( $U_{221,72} = 6035.00$ ,  $p = 0.002$ ). The PARA  
344 increased from 2247.87 to 2827.34 ( $U_{221,72} = 5838.50$ ,  $p < 0.001$ ). The contiguity decreased



345 from 0.41 to 0.30 ( $U_{221,72} = 5959.50$ ,  $p = 0.001$ ). The connectivity values were not significantly  
346 different between years.

347

#### 348 **No-diving marine reserves**

349

350 Out of the four areas, MR1, MR2, nMR1, and nMR2, only the sheltered, no-diving  
351 reserve site (MR2) experienced a positive increase in coral cover over the time period, going  
352 from 66% coral to greater than 83% (Figure 5A). This was accompanied by a decline in sand  
353 from 31% in the early 1980s to 6% in 2008-09 (Figure 5C). MR1, nMR1, and nMR2 all  
354 experienced declines in coral cover and increases in sand (Figure 6). MR2 is the only site that  
355 experienced a decrease in patchiness within the reserve over time (Figure 4), which was  
356 accompanied by increases in the mean patch area and PARA (Figure 5D & 5E). MR1, nMR1,  
357 and nMR2 all experienced increases in the number of patches (Figure 4) and decreases in mean  
358 patch area (Figure 5D), but mean PARA increased in all three (MR1, nMR1, and nMR2; Figure  
359 5E). All four areas experienced declines in contiguity (Figure 5F). Mean connectivity values  
360 decreased in MR2 and nMR1, but increased in nMR2 (Figure 5G). In the early 1980s, there was  
361 only one large coral patch in MR1 so there is no connectivity value. Patch PARAs and contiguity  
362 were not significantly different as a result of year, exposure, status as a marine reserve or any  
363 combination of the three (Table 3). The mean patch area was not significantly impacted by year,  
364 exposure or status as a marine reserve. Connectivity was significantly different between the  
365 groups ( $H = 16.68$ ,  $df = 6$ ,  $p = 0.01$ , adjusted for ties). In the early 1980s, the connectivity of the  
366 non-reserve, exposed site was significantly higher than the sheltered reserve site in the early  
367 1980s (t-test = -5.79,  $df = 7$ ,  $p < 0.001$ ) and in 2008-09 (t-test = -10.446,  $df = 3$ ,  $p = 0.002$ ).

368

369 **Effect of exposure on Klein Bonaire**

370

371 From the early 1980s to 2008-09, the sheltered, eastern portion of Klein Bonaire declined  
372 from 37% coral to 27% (Figures 7A & 8). Between the two time periods the sand/coral mixture  
373 class increased from 6% of the total area to 19% (Figure 7B), while sand declined slightly from  
374 57% to 54% (Figure 7C). The exposed, western side of Klein Bonaire initially had a higher  
375 percentage of coral cover than the eastern side (63%), which declined to less than 15% in 2008-  
376 09 (Figures 7A & 8). This was accompanied by an increase in sand from 35% to 57% and an  
377 increase in the amount of area covered by a sand/coral mixture from 1.5% to 28% (Figure 7B &  
378 7C). The exposed side of the island increased in the number of patches of coral from 8 to 31,  
379 whereas the sheltered side of Klein experienced a decline in the number of coral patches from 14  
380 to 10 (Figure 4).

381 Between the two time periods, only connectivity was significantly different on the  
382 exposed side of the island ( $U_{31,8} = 50.5$ ,  $p = 0.01$ ; Figure 7G). There was no significant effect of  
383 year or exposure on patch area (Figure 7D), PARA (Figure 7E), or contiguity (Figure 7F).  
384 Connectivity was significantly different between the habitat groups ( $H = 7.99$ ,  $df = 3$ ,  $p = 0.05$ ,  
385 adjusted for ties), although, after Bonferroni adjustment (for six pairwise comparisons of the four  
386 habitats:  $\alpha = 0.0083$ ), pairwise comparison (Mann-Whitney Rank Sum Test) found none of the  
387 combinations of year and exposure to be significantly different.

388

389 **DISCUSSION**

390

391 Using satellite remote sensing techniques to determine coral cover on the shallow reefs of  
392 Bonaire (less than 10 m) and comparing it to the atlas created by van Duyl in the 1980s coral has  
393 declined from 62% to only 30% over the time period. However, Bonaire's reefs are experiencing  
394 less severe declines in coral cover than elsewhere in the Caribbean, which have seen declines  
395 from about 50% to 10% hard coral cover in three decades (Gardner et al., 2003, Jackson et al.,  
396 2014). Our findings on current coral cover using remote sensing techniques (30%) are similar to  
397 findings by Steneck et al. (2011 and 2015), which reported 34-39% live cover at quadrats in 10  
398 m of water off the leeward coast of Bonaire and to Stokes et al. (2010) who reported coral cover  
399 ranging from 23.7-38.4% at depths between 10 and 30 m. Bak et al. (2005) reported ~20% coral  
400 cover within permanent quadrats at 10-20 m depth on Bonaire. Jackson et al. (2014) reported  
401 coral cover on Bonaire to be 31% at 10 m depth, which was a decrease of 32% between 1974 and  
402 2008. At 20 m depth cover was much lower, 8%, a decrease of 63% between the same years  
403 (Jackson et al., 2014). Areas of previously high coral cover examined here were replaced mostly  
404 by sand and the remaining coral has become increasingly patchy, with a greater number of small,  
405 less contiguous coral patches. The data for van Duyl (1985) was collected in the early 1980s,  
406 prior to the die-off of large acroporids, which occurred on Bonaire in 1983 (Knowlton et al.,  
407 1981; Jackson et al., 2001; Jackson et al., 2014). On Bonaire rubble created from the broken  
408 calcium carbonate of *Acropora palmata* and *A. cervicornis* is clearly visible particularly in the  
409 shore zone and shallow reef (< 5 m). However, in contrast to other regions in the western  
410 Atlantic, Bonaire has not been severely damaged by hurricanes in recent times (Bries et al.,  
411 2004), but when hurricanes do occur in the region the normally calm leeward coast can  
412 experience higher wave energy (van Duyl, 1985; Pandolfi & Jackson, 2001). In 1999 hurricane  
413 Lenny moved in a rare west-to-east direction across the Caribbean, resulting in coral toppling,

414 fragmentation, tissue damage, bleaching, and smothering along the coast of Bonaire (Bries et al.,  
415 2004). A subsequent study comparing QB satellite images from the years before and after Lenny  
416 could measure the impact of this specific storm on coral cover. Fortunately, Bonaire has not seen  
417 an overgrowth of macroalgae in areas where coral has been lost and replaced by sand and rubble  
418 (Kramer, 2003; pers. obs.), as has been documented elsewhere in the Caribbean (Bellwood et al.,  
419 2004; Bruno et al., 2009).

420         Although most of the reef experienced declines in coral cover, a non-negligible 16% of  
421 the reef did experience positive changes toward higher coral cover, and a large amount, 40%,  
422 remained unchanged between the early 1980s and 2008-09. It was initially surprising to the  
423 authors that the largest amount of increase in coral cover was concentrated along the middle of  
424 the leeward coast, where the capital city of Kralendijk is located and most of the population  
425 resides. In contrast, the much less inhabited northern and southern leeward coasts experienced  
426 higher levels of negative change. The authors expected more negative impacts to be concentrated  
427 around the population center owing to nutrient inputs, sedimentation, and runoff as a result of  
428 development. A possible reason these negative impacts were not found where expected is that  
429 mapping by van Duyl (1985) may have occurred after damage had already taken place as a result  
430 of rapid building and development of the capital city of Kralendijk. In addition, this area of  
431 coastline is sheltered by the neighboring island of Klein Bonaire and the adjacent shore of Klein  
432 Bonaire, which is sheltered by the main island, was also not found to have experienced as drastic  
433 of a decrease in coral cover when compared to the exposed side of the island Klein; it became  
434 less patchy over the time period, with fewer, but larger patches of coral, suggesting that  
435 protection of the coastline may be helping to buffer coral losses and fragmentation. The fact that  
436 the sheltered marine reserve and sheltered side of Klein Bonaire both experienced decreases in

437 the number of coral patches and increases in patch area supports the hypothesis that status as a  
438 marine reserve and sheltering from exposure may buffer against coral fragmentation.  
439 Surrounding Klein Bonaire the majority of coral loss was in the shallower portions of the reef,  
440 along the shoreline (Figure 8). Elsewhere, long stretches of coral patches have been broken up  
441 along the coast over time, as in MR1, MR2 and nMR2 (Figure 6), and coral in the shallowest  
442 part of the reef, along the coast, has been lost.

443 It is not surprising that increases in the number of patches of coral were accompanied by  
444 overall declines in cover and decreases in the size of individual patches. Patches with small  
445 nearest neighbor distances are typically situated in landscapes containing more habitat than are  
446 patches with large nearest neighbor distances, so this measure of isolation is generally related to  
447 amount of total habitat in the landscape (Fahrig, 2003). Connectivity showed positive changes as  
448 the Euclidean nearest neighbor (ENN) value declined over time in the sheltered marine reserve  
449 and in the exposed non-reserve site, but the sheltered non-reserve site experienced an increase in  
450 this value, with a larger number of smaller coral patches spaced farther apart from one another.  
451 Fragmentation *per se* implies a larger number of smaller patches; however, as these changes, in  
452 addition to the change in contiguity and connectivity values, were not significant, this suggests  
453 that habitat fragmentation is less of an issue on Bonaire than habitat loss in general. Fahrig  
454 (2003) suggests that the term “fragmentation” be limited to the breaking apart of habitat,  
455 independent of habitat loss, this can happen on a reef when a large coral patch breaks apart at the  
456 center, but gains area along the outside edges, resulting in no net loss of total habitat; empirical  
457 evidence to date suggests that the loss of habitat has large negative effects on biodiversity.  
458 Recent studies have shown that a variety of impacts can result from habitat fragmentation, it is  
459 unknown whether such impacts are the result of fragmentation itself, the total loss of habitat

460 during fragmentation, degradation of the habitat after the fragments are isolated, or the effect of  
461 isolation itself (Caley et al., 2001). Most studies of habitat fragmentation in the marine  
462 environment have been in seagrass habitats (Eggleston et al., 1998; Hovel & Lipcius, 2001;  
463 Hovel & Lipcius, 2002). Shrimp are more abundant in small patches of seagrasses because a  
464 large perimeter-to-area ratio (PARA) is important for feeding (Eggleston et al., 1998) and a  
465 greater number of invertebrate taxa occur in larger patches of seagrass habitat (Bowden et al.,  
466 2001). Other studies have reported reduced survival in fragmented habitats as a result of  
467 increased exposure to predators along the edges of habitat patches, i.e., a large PARA  
468 (Brittingham & Temple, 1983; Andr n & Angelstam, 1988). These effects of fragmentation  
469 likely vary greatly by species (Eggleston et al., 1998), particularly between invertebrates and  
470 fishes. Although loss of coral habitat on Bonaire is undoubtedly occurring, and the remaining  
471 available habitat is being broken into smaller patches, it is not possible to separate the effects of  
472 loss from fragmentation. Fahrig (2003) suggests that the effects of fragmentation *per se* may be  
473 greater in tropical systems than in temperate systems, but this prediction remains to be tested.  
474 Caley et al. (2001) represents an experimental study on a coral reef at a fine spatial scale and  
475 found habitat degradation to have a much greater detrimental impact than fragmentation, and the  
476 effects of fragmentation in the absence of loss and degradation to be either neutral or positive,  
477 and provides a useful and complementary approach to experiments at macro-landscape scales  
478 such as the present study. Unfortunately, landscape-level analyses of coral cover are lacking and  
479 do not lend well to experimental manipulation, particularly given the current fragile state of coral  
480 reef ecosystems. Satellite remote sensing techniques are a non-invasive method for coarsely  
481 classifying coral reef habitats (Mishra et al., 2006; Relles et al., 2012) rapidly at the landscape  
482 scale to assess changes in coral cover following disturbances such as disease, storms,

483 sedimentation and eutrophication. The present study shows that modern maps created by this  
484 method can be compared to ancillary datasets to assess trends in coral cover over significantly  
485 longer time scales. Increased groundtruthing of the satellite data would be useful for improving  
486 the accuracy of the classification system, specifically the relatively poor user accuracy for the  
487 coral class reported here (50%).

488         Landscape-level analyses such as this are useful for evaluating the success of marine  
489 policy and focusing future management decisions on areas of concern, as coral reef ecosystems  
490 continue to change faster than our current abilities to measure those changes. Based on our  
491 findings the island of Bonaire seems to be doing better than elsewhere in the Caribbean as a  
492 well-managed and long-established Marine Protected Area (MPA). The work completed here can  
493 potentially be used to establish additional no-diving marine reserves by identifying areas that  
494 have maintained relatively high coral cover or have experienced increases in coral over the time  
495 period and also identify areas of concern that have not fared as well and may warrant an  
496 increased level of protection.

497

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686



687 Fig. 1. The islands of Bonaire and Curaçao are located in the Dutch Caribbean, about 80 km  
688 north of Venezuela.

689

690 Fig. 2. The outline map (A) shows the entire island of Bonaire and neighboring island of Klein  
691 Bonaire. The northwest coast of the island (a), the central coast (b), and the southern coast (c) are  
692 inset. The locations of the exposed (MR1) and sheltered (MR2) marine reserves and adjacent  
693 exposed (nMR1) and sheltered (nMR2) non-reserve sites (B). Klein Bonaire showing the  
694 sheltered and exposed sides of the island (C).

695

696 Fig. 3. Changes in percent coral cover (A), sand/coral mixture (B) and sand (C) between the  
697 early 1980s (black) and 2008-09 (white) on the entire leeward coast of the island of Bonaire, the  
698 northwest coast, the central coast, the southern coast, and the uninhabited island of Klein  
699 Bonaire.

700

701 Fig. 4. Changes in the number of coral patches between the early 1980s (black) and 2008-09  
702 white) off the leeward coast of the main island, on the sheltered and exposed sides of Klein  
703 Bonaire, and in the marine reserves and adjacent non-reserve sites. Note: log scale is used and  
704 only one coral patch in the early 1980s in the no-entry marine reserve 1 (MR1).

705

706 Fig. 5. Changes in percent coral cover (A), sand/coral mixture (B) and sand (C) between the  
707 early 1980s (black) and 2008-09 (white) in the two marine reserves (MR1 and MR2) and  
708 unprotected adjacent areas (nMR1 and nMR2) on Bonaire. Note: there was no sand/coral mixture  
709 class in MR1 or nMR1 in the early 1980s. Changes in the patch parameters area (D), PARA (E),

710 contiguity index (F) and ENN distance (G) between the early 1980s (black) and 2008-09 (white)  
 711 in the two marine reserves (MR1 and MR2) and unprotected adjacent areas (nMR1 and nMR2)  
 712 on Bonaire.

713

714 Fig. 6. Coral, sand/coral mixture, and sand classes in the exposed MR1 and nMR1 in the early  
 715 1980s (A) and 2008-09 (B). The negative, neutral and positive change values over the time  
 716 period in MR1 and nMR1 (C). Coral, sand/coral mixture, and sand classes in the sheltered MR2  
 717 and nMR2 in the early 1980s (D) and 2008-09 (E). The negative, neutral and positive change  
 718 values over the time period in MR2 and nMR2 (F).

719

720 Fig. 7. Changes in percent coral cover (A), sand/coral mixture (B) and sand (C) between the  
 721 early 1980s (black) and 2008-09 (white) on the sheltered and exposed portions of Klein Bonaire.  
 722 Changes in the patch parameters area (D), PARA (E), contiguity index (F) and ENN distance (G)  
 723 between the early 1980s (black) and 2008-09 (white) on the exposed and sheltered sides of the  
 724 island. Only the change in ENN distance over the time period on the exposed side of the island  
 725 was significant ( $U_{31,8} = 50.5, p = 0.01$ ). \* indicates a significant difference between time  
 726 periods. Error bars indicate  $\pm$  two standard errors.

727

728 Fig. 8. Coral, sand/coral mixture, and sand classes on the western, exposed coast (left) and on the  
 729 eastern, sheltered coast (right) of Klein Bonaire in the early 1980s (A) and 2008-09 (B). The  
 730 negative, neutral and positive change values over the time period along the exposed coast (C).

731

732

733

734 Table 1. Van Duyl’s classifications on the left reclassified into the coarser classification system  
 735 discernible by the satellite remote sensing method for the 2008-09 maps. Coral cover greater  
 736 than 20% (van Duyl, 1985) was classified as coral under the coarser classification system and  
 737 sand cover greater than 50% (van Duyl, 1985) was classified as sand.

738

<b>Van Duyl’s class</b>	<b>Coarse class system</b>
Sea Whip	Sand/Coral
<i>Acropora cervicornis</i> (>20%)	Coral
<i>Acropora palmata</i> (>20%)	Coral
Finger/Foliate coral group (>20%)	Coral
Head coral group (>20%)	Coral
<i>Acropora cervicornis</i> ( < 20%)	Sand/Coral
<i>Acropora palmata</i> ( < 20%)	Sand/Coral
Finger/Foliate coral group ( < 20%)	Sand/Coral
Head coral group ( < 20%)	Sand/Coral
Plant	Sand/Coral
Rubble	Sand
Sand	Sand
Shorezone	Sand

739

740

741 Table 2. Change values calculated in ArcGIS representing changes in bottom type between the  
 742 early 1980s and 2008-09, distinguishing positive, negative and no change.

743

<b>Value</b>	<b>Change (from-to)</b>	<b>Change (type)</b>
11	Coral to Coral	None
12	Sand/coral to Coral	Positive
13	Sand to Coral	Positive
21	Coral to Sand/coral	Negative
22	Sand/coral to Sand/coral	None
23	Sand to Sand/coral	Positive
31	Coral to Sand	Negative
32	Coral/sand to Sand	Negative
33	Sand to Sand	None

744

745

746 Table 3. F-stats and p-values resulting from a three-way ANOVA with year, exposure and  
 747 marine reserve status as predictors for the variables PARA and CONTIG (df = 29).

748

	PARA		CONTIG	
	F	p	F	p
Year	3.63	0.07	3.07	0.09
Exposure	0.53	0.47	0.81	0.38
Reserve	0.17	0.69	0.12	0.74
Year x Exposure	0.86	0.36	1.20	0.28
Year x Reserve	0.11	0.74	0.07	0.80
Exposure x Reserve	1.40	0.25	1.29	0.27
Year x Exposure x Reserve	0.00	1.0	0.00	0.95

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