Seagrass cover expansion off Caja de Muertos, Puerto Rico, as determined by long-term analysis of historical aerial and satellite images (1950 – 2014)

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Abstract

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Seagrass ecosystems affected by climate change and anthropogenic disturbances require baseline characterization of their cover, distribution, and dynamics for effective conservation strategies. Caja de Muertos (CM) is an important nature reserve in Puerto Rico where long-term trends in seagrass cover are unknown but where availability of historical aerial photographs can provide elements for analyzing seagrass dynamics. The purpose of this study was to understand those dynamics in CM, thereby providing a baseline for determining the severity of future disturbances and inform conservation strategies. We quantified changes in seagrass spatial extent using object-based image analysis in a 2014 WorldView-2 image and historical aerial photographs from 1950 to 2010. Contrasting with worldwide seagrass declining trends, seagrass extent in CM showed a positive rate of expansion and increased 64%, which was mainly explained by the patchy seagrass cover category that was also the most persistent cover throughout the 64-year period analyzed. Findings suggest an increase in seagrass extent due to recolonization of seagrasses after impacts of tropical storm Baker in 1950, aided by other factors such as reduction in grazing pressure. Even though seagrass cover expanded, with other tropical storms and hurricanes, no negative effects were observed except between 1993 and 1999. The amount and frequency of changes in seagrass cover categories varied between zones and seemed to be linked to localized environmental conditions (e.g. wave exposure) and geomorphological characteristics. The present study represents a baseline of seagrass cover distribution, and dynamics offering valuable information for conservation strategies in Caja de Muertos Island Nature Reserve. In the absence of *in situ* long-term monitoring data, this study also shows how aerial photography and an object-based image analysis are effective for assessing trends and quantifying seagrass cover changes in clear oligotrophic waters.

Keywords: seagrass dynamics, aerial photography, WorldView-2, object-based image analysis, hurricanes, Caribbean

Highlights

- Historical aerial photography was used to reconstruct seagrass distribution.
- Seagrass cover followed a positive rate of expansion over six decades.
- Seagrasses may have recolonized after impacts of tropical storm Baker in 1950.
- Hurricanes Hortense and Georges probably caused a decrease of seagrass extent.
- Wave exposure and geomorphology caused variations between different seagrass beds.

1 Introduction

Seagrasses represent a highly productive and ecologically relevant marine community (Zieman and Zieman, 1989), providing many ecosystem services (Nordlund et al., 2016) such as sediment stabilization, and nursing and feeding grounds for many organisms (Duarte, 2002; Himes-Cornell et al., 2018; Waycott et al., 2009). Worldwide, both natural and anthropogenic factors have influenced the decline of seagrass beds (Carlson et al., 2018; Duarte, 2002; Orth et al., 2006, Ruiz-Frau et al., 2017, Wilson et al., 2018). For instance, human activities, such as dredging and filling, boating, nutrient enrichment, and sedimentation have detrimental effects on seagrass communities (Miller and Lugo, 2009; Orth et al., 2006; Santos et al., 2016; Unsworth et al., 2018). Furthermore, in the Caribbean and other tropical areas, hurricanes and tropical storms represent a natural hazard for seagrass communities by causing sediment erosion and/or deposition on seagrass beds (Creed et al., 2003).

In a scenario of increasing threats to seagrass communities, there is a need to understand seagrass spatial dynamics at different temporal scales. Information on long-term trends in seagrass distribution can improve conservation strategies of these habitats (VIMS, 2018). However, data on seagrass dynamics have been available mainly through *in situ* monitoring (Erftemeijer and Herman, 1994; Gallegos et al., 1993; Lanyon and Marsh, 1995) and in places as Puerto Rico, repeated field observational records are uncommon or inexistent. Alternatively, remote sensing has been used for monitoring changes in seagrass beds (Armstrong, 1981, 1993; Kendall et al., 2001; Kendrick et al., 2002; Lyons et al., 2011; Moore et al., 2001; Pu and Bell, 2013; Roelfsema et al., 2009), although its use is dependent on suitable spatial and temporal availability of imagery (Uhrin and Townsend, 2016). In many occasions, aerial photography may represent the only available source of information for long-term analysis of seagrass beds. The combination of high spatial resolution, large spatial extent, and long temporal coverage makes historical aerial photographs the largest source of information available for research on long-term vegetation dynamics (Kadmon and Harari-Kremer, 1999).

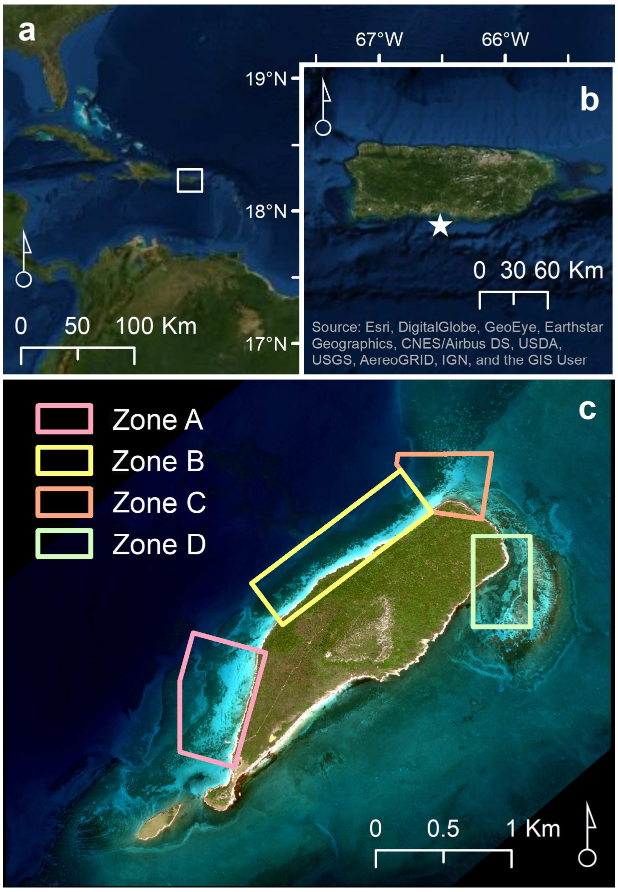
Caja de Muertos Island in Puerto Rico is an example of an ecologically important nature reserve where the long-term trends in seagrass spatial cover are unknown and where historical aerial photographs may provide a long-term record for analyzing seagrass dynamics. Although the spectral information these photographs provide is limited, the clear oligotrophic waters that surrounds this island (León-Pérez et al., 2019) provide the possibility of differentiating seagrass beds from other benthic features. A preliminary analysis of this historical dataset revealed an increase in seagrass extent, contrasting with worldwide trends (Orth et al., 2006). Knowledge about the spatial distribution and trends in seagrass can guide future management decision in the reserve.

This study follows a previous work characterizing seagrass communities in Caja de Muertos Island (León-Pérez et al., 2019) and uses historical aerial photography and satellite data to reconstruct the historical distribution of seagrass beds. The purpose of this study was to understand long-term spatial and temporal dynamics of seagrass beds (i.e. spatial cover) and quantify changes in aerial extent from 1950 to 2014 to provide baseline information for managers to determine the severity of possible future natural and/or anthropogenic impacts in these habitats. The analysis was conducted in four zones around the island where historical aerial photography was available.

2 Methodology

2.1 Study area

The Caja de Muertos Island Nature Reserve (CMINR) is a 57 km^2 protected area composed by an island (Caja de Muertos) and two keys (Cayo Morillito and Cayo Berbería), located off the southern coast of Puerto Rico (Fig. 1). This study focused on Caja de Muertos Island due to the availability of long-term records of aerial photographs. Caja de Muertos Island (17°53’36"N, 66°31’15"W) is approximately 2.75 km long by 0.85 km wide (at its widest point), and oriented approximately at a 45-degree angle from its southernmost tip on the southwest towards the northeast. Its west side is protected from the dominant incoming wind and wave energy direction, which is mainly from the East and Southeast. The climate is characterized by dry (December to April) and rainy seasons (May to November) (Glynn, 1973).



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AereoGRID, IGN, and the GIS User

Fig. 1. Caja de Muertos Island Nature Reserve showing location of study areas: (a) Caribbean Sea and Puerto Rico (white rectangle); (b) Puerto Rico and Caja de Muertos Island (star); (c) WV-2 image of Caja de Muertos Island and the four zones selected for the long-term analysis of seagrass distribution.

2.2 Image Acquisition and Pre-Processing

Ten historical aerial photographs from CMINR (from 1950 to 2010), mostly black and white (panchromatic) were obtained from different sources (Table 1, Fig. A.1). The spectral resolution varied among them; however, all except one (1999) had a pixel size of 1m or less. In addition, a WorldView-2 (WV-2) satellite image from October 16, 2014 was also used, which consisted of a single panchromatic band with a spatial resolution of 0.5 m. Similarities between the spatial and spectral resolution allowed for the use of these two types of remote sensing data (WV-2 and aerial photographs) in the analysis. We pre-processed the photographs using ArcMap 10.1 (ArcGIS®) having a pixel size downscaled to a spatial resolution of 1 m, except for the 1999 photograph, which was rescaled from 2.4 m to 1 m. All photographs were georeferenced (e.g. spatially rectified) to a projected coordinate system for Puerto Rico and the US Virgin Islands (NAD 1983 HARN State Plane Puerto Rico Virgin Islands FIPS 5200), by matching ground control points between aerial photographs and the WV-2 2014 panchromatic image (e.g. base-map). The root mean square error (RMS) was calculated for each georeferenced photo (Table 1) to determine how consistent the transformation was between the control points used during the georeferencing process (ESRI, 2009). Photographs from years 1950 and 1964 were mosaicked.

Year	Original Spatial Resolution (m)	Source	RMS
1950	0.4	USGS	0.43
	0.4	USGS	0.37
1967	0.7	USGS	0.82
	0.7	USGS	
1977	1.0	N/A	0.96
1993	1.0	USDA	0.50
1999	2.4	N/A	0.53
2004	1.0	USACE	0.86
2007	0.3	USACE	0.88
2010	0.3	USGS	0.55
2014	0.5	Digital Globe	N/A

Table. 1 Historical record of imagery from Caja de Muertos Island. RMS = root mean square error; USGS = United States Geological Survey; USDA = United States Department of Agriculture; USACE = United States Army Corps of Engineers; N/A = information not available.

2.3 Photointerpretation of Historic Aerial Photography

Both the WV-2 panchromatic band and the historical aerial photograph record were analyzed using an object-based image analysis (OBIA). The OBIA approach considers the spectral, spatial, textural and topological characteristics of the image data and consist of two main procedures: segmentation, and classification (Lang, 2008). We selected this approach because it has the potential to increase seagrass percentage cover mapping (Roelfsema et al., 2014), and it has been previously used to accurately map seagrass cover (León-Pérez et al., 2019; Lyons et al., 2012).

The first step of the analysis consisted on using the multi resolution segmentation algorithm embedded in the software eCognition Essentials 1.2 (Trimble®) to segment the images into objects (polygons). This segmentation process includes three user-selected parameters: scale, shape, and compactness. After an iterative trial and error process (Lathrop et al., 2006), a series of segmentation parameters were established and used for the entire historical record. The first step was to use a coarse segmentation (scale 100; color/shape 0.05; smoothness/compactness 0.4) in order to select objects containing seagrass, followed by a re-segmentation into smaller objects (scale 35; color/shape 0.05; smoothness/compactness 0.4) in order to eliminate non-seagrass areas. The final segmentation (scale 70; color/shape 0.05; smoothness/compactness 0.4) was used to further classify seagrass objects into continuous and patchy areas. This analysis was conducted in descending chronological order, from 2014 to 1950.

Afterwards, we visually classified objects using black and white aerial photography and the panchromatic band of the 2014 WV-2 image. A 2014 benthic map (León-Pérez et al., 2019) was used as a reference to classify seagrass areas, which were mostly composed of a combination of *Thalassia testudinum* and *Syringodium filiforme*. When possible, the 2014 true color image and color photographs from years before 2014 were used as a visual aid in areas where seagrass and macroalgae were difficult to differentiate between each other. Areas where seagrass classification was confusing were not analyzed. Some photographs had no raster information (no data) for some areas, thus prevented analysis for the entire study area. Consequently, the assessment of the long-term changes in seagrass extent was only conducted within four zones (Fig. 1), which were the only areas having continuous data for all the years between 1950 and 2014. In order to include the year 2010 in the analysis, we split the elongated seagrass bed located northwest of Caja de Muertos Island into Zones B and C. The 2010 photograph had significant sunglint that prevented the determination of seagrass extent in Zone C for that year.

2.4 Data Analysis

A linear mixed-effect model (LME) with a random intercept term was used to statistically model trends in overall total seagrass cover between 1950 to 2014. Year was treated as a continuous variable and zone was treated as a random blocking factor since we were not interested in the effect of zone on total seagrass area. Tukey's test for non-additivity was used to test for interactions since there was only one replicate per interaction level, and a significance level of 0.1 was used to reduce the risk of Type II error. Assumptions for the LME were visually examined with QQ plots and a significance level of 0.05 was used for LME test. The regression was plotted with 95% confidence bounds and Cox and Snell pseudo R-squared was calculated.

The Change Detection tool in eCognition was used for analyzing the overall differences in seagrass distribution between 1950 and 2014. Differences in seagrass extent between each period (e.g. 1950-1967) was calculated in ArcMap using geoprocessing tools (e.g. union), data management tools (e.g. calculate field), and the calculate geometry dialog. Radar plots were constructed for each individual zone and an additional radar plot was generated to represent all zones combined. The data were standardized by dividing the categorized area in each period by the maximum colonizable area for that zone (or all zones) to show which change dominated during each period. The total colonizable area (i.e. maximum extent) was calculated by overlaying all mapping results of seagrass extent for the time series and tracking the outer boundary of the seagrass beds (Frederiksen et al., 2004). Categories represented in the radar plots are: complete loss (areas that lost seagrass cover), from continuous to patchy (areas that decrease cover category), unchanged (areas that stayed with the same cover category), from patchy to continuous (areas that increase cover category), and new areas (areas where seagrass emerged).

Additionally, a map of seagrass persistence was created on a per-pixel basis in ArcMap to show the most frequently occurring (modal) seagrass category for each pixel thought the time series (Lyons et al., 2013). This metric provides information about which seagrass category dominated from 1950 to 2014. In order to evaluate the dynamics of change of these seagrass beds, we measure the amount of variation from the most frequently occurring pixel (Lyons et a., 2013). We used two spatial statistics for the creation of the seagrass cover level variability map: range (difference between the largest and smallest value in the time series for that pixel) and the number of times the values in the time series were not equal to the persistence value for that pixel. From now on, the former is referred to as fluctuation and the later as frequency of variation. We combined these two metrics into five categories described in Table 2. The percentage calculated for both the persistence and the variability analysis was also based on the total colonizable area (for each of the zones or for the whole study area).

Seagrass Cover Variability Category	Category Full Name	Description

no variability	no variability	Pixels that did not change cover category throughout the time series.
LFIV	lower fluctuation, infrequently variable	Pixels that changed to another cover category (had two cover categories in the time series) and experienced few events of change (< 3).
LFFV	lower fluctuation, frequently variable	Pixels that changed to another cover category and experienced frequent events of change (4-5).
HFIV	higher fluctuation infrequently variable	Pixels that fluctuated between more than two categories (had continuous, patchy and no cover in the time series) and experienced few events of change.
HFFV	higher fluctuation, frequently variable	Pixels that fluctuated between more than two categories and experienced frequent events of change.

Table. 2 Categories used for the creation of the seagrass cover variability map.

3 Results

From 1950 to 2014, the area covered by seagrass changed from 0.326 to 0.534 km^2 (Table 3), representing a 64% overall increase. The overall rate of increase was 0.001 km^2/year where 95% of seagrass areas had a growth rate between -0.151 and 0.152 km^2/year as showed by the 95% confidence intervals in Fig. 2 ($p < 0.0001$). Most of this increase constituted patchy seagrass areas that increased 124%, following by a 23% increase of continuous seagrass areas (Table 3). In general, in all zones except Zone B, the patchy seagrass cover category comprised more area than the continuous seagrass cover category throughout the studied period (Fig. B.1).

		Seagrass Area (km^2)																
	Category	**1950**		**1967**		**1977**		**1993**		**1999**		**2004**		**2007**		**2010**		**2014**
Zone A	Continuous	0.007	(49)	0.011	(52)	0.016	(55)	0.025	(-68)	0.008	(23)	0.010	(-49)	0.005	(304)	0.021	(13)	0.024
	Patchy	0.052	(9)	0.056	(71)	0.096	(33)	0.128	(-26)	0.095	(28)	0.121	(6)	0.128	(-16)	0.108	(12)	0.120
	Total	0.059	(14)	0.067	(68)	0.113	(36)	0.153	(-33)	0.103	(27)	0.131	(2)	0.133	(-3)	0.128	(12)	0.144
Zone B	Continuous	0.170	(-32)	0.116	(32)	0.153	(31)	0.200	(-36)	0.129	(32)	0.170	(1)	0.173	(2)	0.177	(-1)	0.175
	Patchy	0.038	(175)	0.104	(-41)	0.061	(0)	0.061	(64)	0.100	(-29)	0.071	(-33)	0.047	(14)	0.054	(19)	0.065
	Total	0.207	(6)	0.219	(-3)	0.213	(22)	0.261	(-12)	0.229	(5)	0.241	(-9)	0.220	(5)	0.231	(4)	0.240
Zone C	Continuous	0.018	(-11)	0.016	(-68)	0.005	(707)	0.040	(-40)	0.024	(72)	0.041	(-20)	0.033	N/A	N/A	(26)	0.041
	Patchy	0.041	(14)	0.047	(78)	0.083	(-32)	0.057	(2)	0.058	(-14)	0.050	(-12)	0.044	N/A	N/A	(-13)	0.038
	Total	0.059	(6)	0.062	(41)	0.088	(10)	0.097	(-15)	0.082	(11)	0.091	(-16)	0.077	N/A	N/A	(3)	0.079
Zone D	Continuous	0.000	(0)	0.000	(*)	0.010	(42)	0.014	(68)	0.024	(55)	0.036	(-50)	0.018	(-14)	0.016	(-100)	0.000
	Patchy	0.001	(6772)	0.050	(10)	0.055	(-4)	0.053	(-14)	0.046	(-34)	0.030	(60)	0.048	(3)	0.050	(43)	0.071
	Total	0.001	(6772)	0.050	(30)	0.065	(3)	0.067	(3)	0.069	(-4)	0.067	(0)	0.066	(-2)	0.065	(9)	0.071
Total	Continuous	0.195	(-27)	0.142	(29)	0.184	(52)	0.280	(-34)	0.185	(40)	0.258	(-11)	0.229	(-7)	0.213	(13)	0.240
	Patchy	0.131	(96)	0.257	(15)	0.296	(1)	0.299	(0)	0.298	(-9)	0.271	(-1)	0.267	(-21)	0.212	(39)	0.294
	TOTAL	0.326	(23)	0.399	(20)	0.479	(21)	0.579	(-17)	0.483	(10)	0.529	(-6)	0.496	(-14)	0.425	(26)	0.534

Table 3. Seagrass areas (in km^2) within all the zones from 1950 to 2014. Numbers in parenthesis represent percent change between adjacent years. Zone C had no data for 2010. Therefore, the percent change was calculated between 2007 and 2014. * This value resulted in an undefined number because of a division by zero.

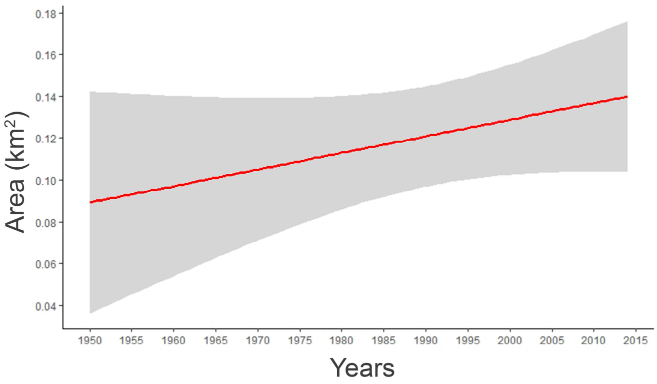


Fig. 2 Overall rate of change (slope = 0.001 km^2/year) of seagrass extent from 1950 to 2014 (Cox and Snell pseudo R^2=0.47; $p < 0.0001$). Seagrass areas had a growth rate between -0.151 and 0.152 km^2/year as showed by the 95% confidence intervals.

Spatial differences in seagrass distribution between 1950 and 2014 are shown in Fig. 3. Overall, more than half of the area covered by the patchy and continuous seagrass areas remained unchanged (57%). Few areas experienced complete loss (4%), while new seagrass areas represented 31%. Some areas transitioned from patchy to continuous seagrass category (3%) or vice versa (6%). When looking at the complete historical record, some variations in seagrass extent were observed between years and between zones.

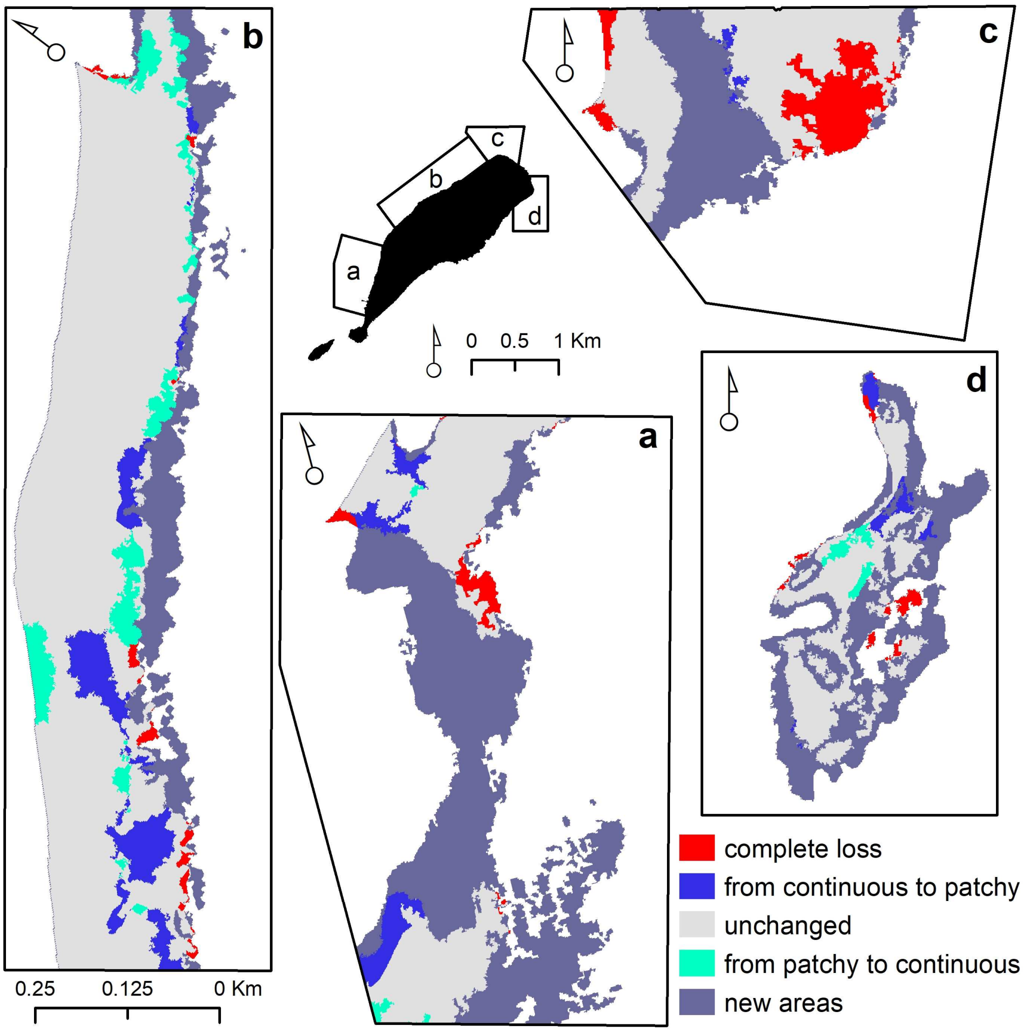
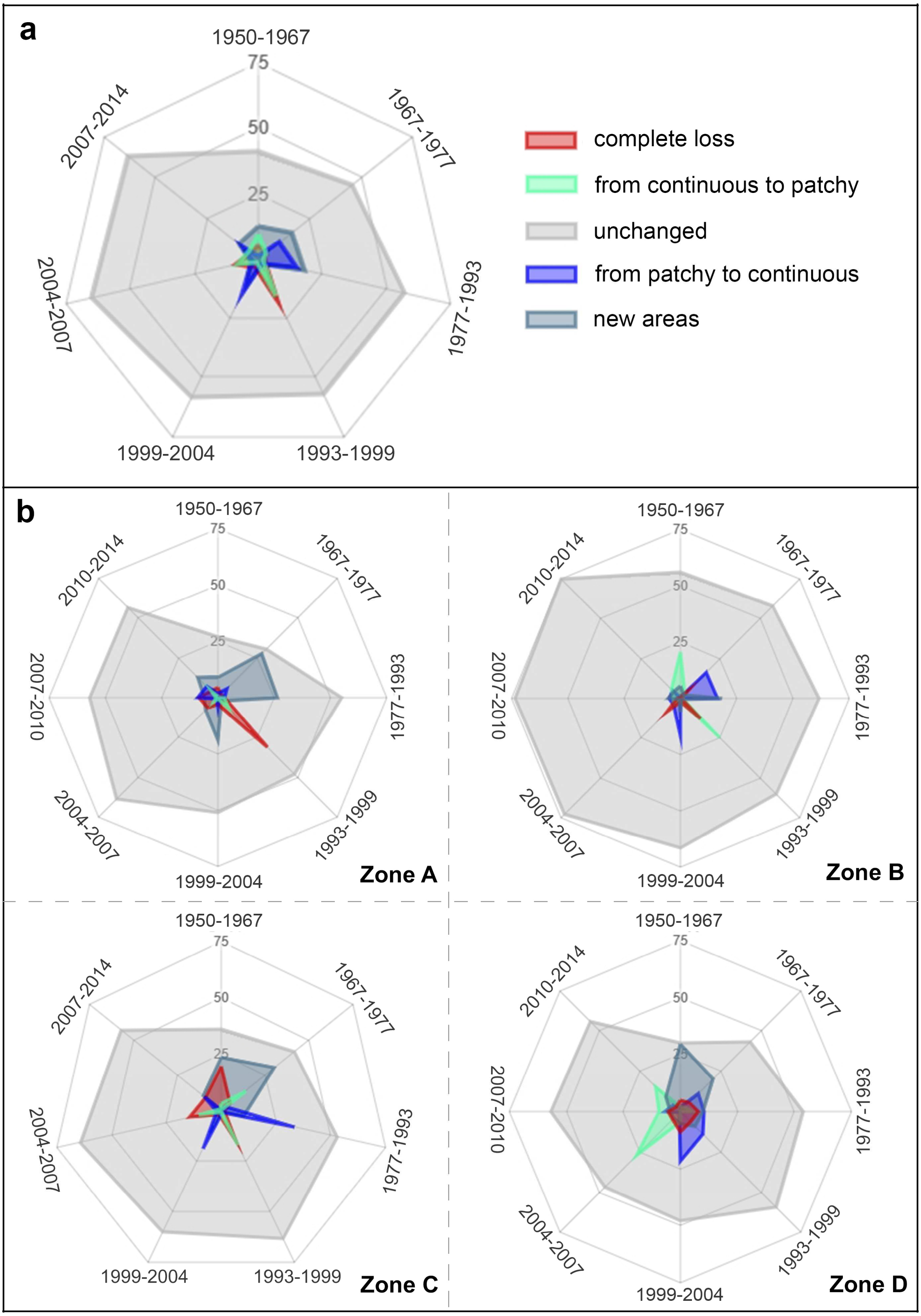


Fig. 3 Overall change in seagrass distribution and category per zone between 1950 and 2014 off Caja de Muertos, Puerto Rico: (a) Zone A, (b) Zone B, (c) Zone C, and (d) Zone D.

All zones showed an increase in seagrass cover from 1950 to 1993 (Fig. 4, Table 4). Some areas originally with a patchy seagrass category changed to the continuous seagrass category (26%). Periods after this increase, showed loss of seagrass area and decrease in seagrass cover from continuous to patchy followed by the emergence of new seagrass areas and the increase in cover from patchy to continuous (visualized by star-like pattern in radar plots, Fig. 4). The first and greatest period of decrease occurred in 1993-1999 and was characterized by the decrease in cover category (transition from continuous to patchy seagrass beds) of 15% and the complete loss of 0.109 km^2 (17%) of seagrass area. A small increase in new seagrass areas (10%) and the change from patchy to continuous (14%) occurred during the period of 1999-2004. a slight decrease in seagrass extent (9%) was documented for the period of 2004-2007 accompanied by a decrease in seagrass cover category (8%). This period had the highest percentage (65%) of unchanged (area that did not experience change in cover category) seagrass areas. In the final period (2007-2014), new seagrass areas increased by 0.059 km^2 (9%) and 8% of seagrass changed from patchy to continuous cover. When observing the entire time series, seagrass areas that remained unchanged represented the highest percentage for each period and increased over time.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Zone D

Fig. 4 Changes in seagrass cover category between periods from 1950 to 2014: (a) overall change (all zones), (b) changes within each zone. Numbers inside plots represent percentages based on total colonizable area for all zones (a) and for each zone (b).

Period	Cover Change Category	Cover Change Percentage (%)				
		Zone A	Zone B	Zone C	Zone D	All Zones
1950-1967	complete loss	4.30	0.99	19.54	4.97	5.44
	from continuous to patchy	0.35	20.27	3.20	2.08	9.51
	unchanged	26.79	55.87	36.21	29.93	41.08
	from patchy to continuous	1.99	0.35	0.00	1.75	0.94
	new areas	8.86	5.56	23.26	29.53	12.53
1967-1977	complete loss	2.07	4.74	4.81	5.73	4.14
	from continuous to patchy	0.08	3.17	13.89	3.00	4.01
	unchanged	30.47	57.92	41.42	43.15	45.59
	from patchy to continuous	5.37	16.22	2.54	11.42	10.33
	new areas	27.83	2.40	30.26	19.99	16.37
1977-1993	complete loss	3.21	0.66	1.62	7.72	2.47
	from continuous to patchy	2.84	0.99	0.02	5.56	1.97
	unchanged	54.83	61.40	53.03	53.79	57.20
	from patchy to continuous	2.86	16.65	33.44	10.49	14.66
	new areas	26.33	18.58	10.33	9.80	18.26
1993-1999	complete loss	30.99	12.78	15.08	6.26	17.39
	from continuous to patchy	7.26	24.87	16.97	0.01	15.34
	unchanged	48.25	59.97	63.41	59.41	57.16
	from patchy to continuous	0.37	0.02	1.37	13.96	2.19
	new areas	2.23	0.77	0.39	8.92	2.21
1999-2004	complete loss	2.95	1.56	2.47	8.67	3.05
	from continuous to patchy	0.57	0.83	1.06	4.21	1.24
	unchanged	50.77	66.61	59.78	47.66	58.54
	from patchy to continuous	3.83	16.62	18.83	21.76	14.07
	new areas	18.83	6.05	11.23	5.61	10.41
2004-2007	complete loss	6.71	8.76	14.58	4.70	8.58
	from continuous to patchy	2.83	4.23	10.07	27.18	7.84
	unchanged	63.96	72.53	64.34	46.80	65.37
	from patchy to continuous	0.50	4.59	1.90	0.55	2.47
	new areas	7.91	0.93	0.52	4.45	3.29
2007-2010	complete loss	8.56	1.31	n/a	5.60	n/a
	from continuous to patchy	0.89	2.84	n/a	9.58	n/a
	unchanged	56.77	73.33	n/a	56.76	n/a
	from patchy to continuous	8.97	4.79	n/a	7.04	n/a
	new areas	6.13	5.43	n/a	4.42	n/a
2007-2014	complete loss	n/a	n/a	8.86	n/a	3.52
	from continuous to patchy	n/a	n/a	0.92	n/a	4.43
	unchanged	n/a	n/a	57.23	n/a	63.46

	from patchy to continuous	n/a	n/a	9.82	n/a	7.56
	new areas	n/a	n/a	10.32	n/a	9.42
2010-2014	complete loss	4.39	0.77	n/a	2.45	n/a
	from continuous to patchy	4.37	5.85	n/a	15.24	n/a
	unchanged	56.78	74.65	n/a	56.13	n/a
	from patchy to continuous	7.22	5.14	n/a	3.98	n/a
	new areas	13.06	4.04	n/a	9.33	n/a

Table 4. Changes in seagrass cover per zone and overall from 1950 to 2014. Cover changes percentages were calculated based on the maximum colonizable area for each zone and for the total study area (see Methods). n/a: calculation was not conducted because of the missing value in Zone C for 2010.

Variations between zones (Fig. 4) indicated that not all zones followed the above-mentioned patterns of seagrass change. Zones A, C, and D seemed more dynamic than Zone B, which showed the highest proportion of unchanged seagrass area among all zones (Table 4) and the highest proportion of the continuous cover category vs patchy (Fig. B.1). During the initial period of increase (1950-1993), all zones experienced an increase in the unchanged category and seagrass areas mostly emerged in Zones A, C, and D.

The seagrass persistence map (Fig. 5) showed the most frequent seagrass category throughout the 64-year study period for each pixel. Patchy seagrass represented the most persistent seagrass category in the study area (43%) followed by the continuous category (36%). In most of the zones (A, C, and D), patchy seagrass cover was also the most persistent seagrass cover (62%, 53% and 58%, respectively). However, in Zone B the continuous seagrass category dominated (63%). Less than one quarter of the total colonizable area (19%) consisted of areas where seagrass was present at a certain year(s) but did not dominate through the studied period. These no seagrass persistence areas were generally located towards the outer shallower edges of the seagrass beds and were more prevalent in Zone A where it represented the second most prevalent seagrass cover (29%). During the creation of the seagrass persistence map, some pixels did not return a value because no category dominated over the other for those pixels (e.g. 4 years patchy, 4 years continuous, 1 year no seagrass cover). These pixels where classified as no data and represented 2% of the total colonizable area (Table 5).

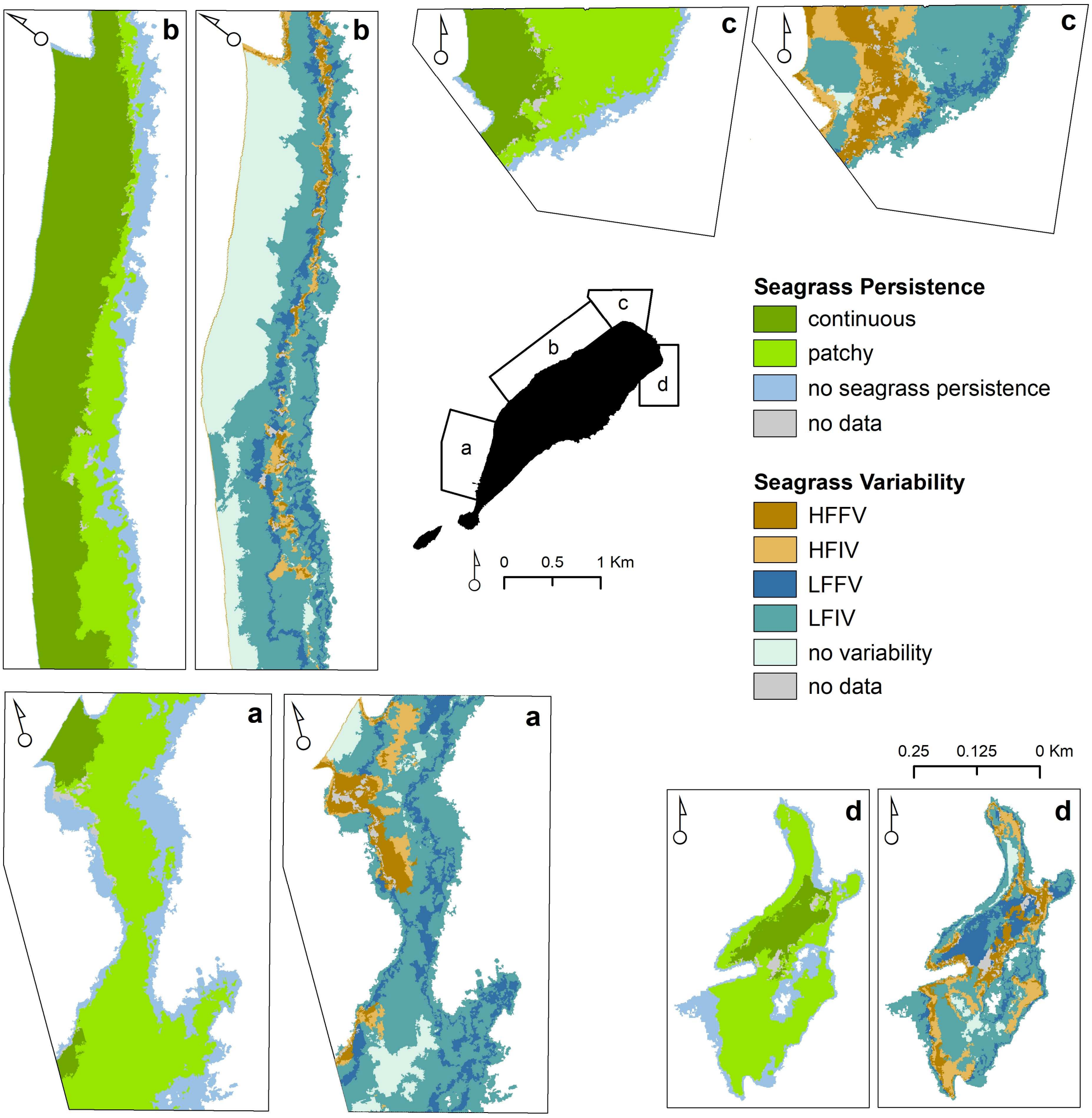

Fig. 5 Seagrass persistence and seagrass cover variability from 1950 to 2014: (a) Zone A, (b) Zone B, (c) Zone C, and (d) Zone D. Seagrass persistence is the most frequently occurring seagrass category over the studied time frame (left side of each pair). Seagrass cover variability

represents the amount of variation from the most frequently occurring pixel (right side of each pair).

Category	Seagrass persistence (%) Zone A	Zone B	Zone C	Zone D	All Zones
Patchy	62.14	21.69	53.22	57.76	42.93
Continuous	7.67	63.47	32.42	15.32	36.39
No seagrass persistence	28.77	13.76	11.81	23.35	18.94
No data	1.42	1.08	2.55	3.58	1.75

Category	Seagrass cover variability (%) Zone A	Zone B	Zone C	Zone D	All Zones
HFFV	7.49	3.58	21.49	12.49	8.75
HFIV	6.33	3.92	17.27	14.38	8.14
LFFV	14.96	8.38	6.80	16.69	11.08
LFIV	60.47	48.64	49.47	48.26	52.04
No variability	9.34	34.40	2.43	4.60	18.24
No data	1.42	1.08	2.55	3.58	1.75

Table 5. Percentages of seagrass persistence and seagrass cover variability from 1950 to 2014. Percentages were calculated based on the maximum colonizable area for each zone and for the total study area (see Methods).

Fig. 5 also shows the variability of seagrass cover throughout the study period. Of the total colonizable area, 18% did not experienced fluctuations in seagrass cover (Table 5). These areas were mainly located in Zone B where it represented 34%. More than half of the total colonizable area experienced low and infrequent variations in seagrass cover (52%). The zones where seagrass variated the most where Zones C (95%), D (92%) and A (89%). However, the highest fluctuations and frequency of variation in seagrass cover was observed in Zone C (21%). A thin line of high variability pixels along the offshore edge of seagrass beds of Zone A, B and C are were caused by a mapping error during the analysis.

4 Discussion

Seagrass habitats are dynamic across space and time (Lyons et al., 2013) in the marine ecosystem and understanding their changes is helpful to implement conservation strategies for their protection (VIMS, 2018). We used a 64-year record of historic aerial photographs and satellite data off Caja de Muertos, Puerto Rico to reconstruct the historic distribution of seagrass beds within four zones and to assess long-term changes in seagrasses cover. Results showed a positive rate of seagrass expansion, where patchy seagrass cover dominated, although variations between years and zones were observed.

4.1 Seagrass distribution and temporal trends

Worldwide, long-term seagrass studies have documented declines and losses due to environmental, biological, and extreme climatological events (Orth et al., 2006). Contrary to these trends in decreasing seagrass cover, our study showed that from 1950 to 2014 seagrass cover increased in Caja de Muertos Island. Similar results were obtained by Armstrong (1981) off La Parguera, Puerto Rico, where seagrass area increased 170% over a period of 43 years, and by Hernández-Cruz et al. (2006) who documented a seagrass cover increase of 89% over a 64-year period off Vieques, Puerto Rico. Hernández-Cruz et al. (2006) suggested that seagrass habitats in Bahía Salina del Sur followed the Principle of Lateral Continuity stated by Rankey (2002), in which seagrass may extend in all directions until reaching a physical barrier, another type of sediment, or is eroded. Given our study quantified an increase in seagrass cover, the question is which were the processes that took place in Caja de Muertos Island resulting in the spatial increase in seagrass cover?

Several factors influencing seagrass colonization, distribution, and expansion may have played a role in our findings. Seagrass succession is characterized by an initial rapid dendritic growth of clones, which is later followed by a compact and slower growth as the seagrass bed reaches a steady state (Sintes et al., 2006). In Caja de Muertos Island, the patchy seagrass cover, which is fragmented and less compacted, dominated the time series both spatially and temporally. During the initial growth period from 1950 to 1993 not just new seagrass areas emerged, but patchy seagrass areas changed to continuous cover apparently following a guerilla strategy. This latter term is used in ecology to describe the early dendritic patterns of growth observed in early succession of clonal species (Lovett-Doust, 1981).

The area susceptible of colonization by seagrass, depend on a series of physical factors such as light availability, substrate type, and wave energy (Gonzalez-Liboy, 1979; Miller and Lugo, 2009). León-Pérez et al. (2019) suggest that light availability is not a limiting factor for seagrass colonization in Caja de Muertos and that seagrass beds within our studied zones colonized over sandy bottoms. Impacts of wave energy on seagrasses was also evidenced by the presence of “blow-outs”, which are small rounded depressions caused by strong wave energy at North of Caja de Muertos Island (Zone C) (León-Pérez et al., 2019). However, a similar case of seagrass coverage expansion was documented for *S. filiforme* in Buck Island Channel, St. Croix, US Virgin Islands, from 1971 to 1999 (Kendall et al., 2004), where increasing seagrass meadow extent was coincident with a greater frequency of hurricanes in the region. These authors argued that given no clear causal mechanism of such seagrass expansion was identified, it is possible that wave energy generated by hurricanes stimulate seagrass growth by fostering seed dispersal and propagation.

Given that high wave energy events in the ocean, such as hurricanes, regulate seagrass distribution (Creed et al., 2003; Glynn et al., 1964; Rodriguez et al., 1994), we explored a dataset from NOAA Hurricane Historical Track record (NOAA, 2019) to consider the potential impacts of cyclonic events in Puerto Rico (Fig. 6). This dataset showed tropical storms and/or hurricanes passing through or near Caja de Muertos Island in all but two periods analyzed (1967-1977 and 2004-2007). We found a decrease in seagrass cover during 1993-1999 coinciding with two hurricanes passing Puerto Rico: Hurricane Hortense (category 1) and Hurricane Georges (category 3). We cannot attribute the slight decrease in seagrass cover observed during the period of 2004 and 2007 to effects of cyclonic events since none were reported during this latter period. In effect, the absence of major wave energy disturbances during this latter period could have influenced the high percentage of seagrass areas having no change in cover category (Table 4). We found that seagrass aerial extent increased during 1950 and 1993 even with tropical storms and hurricanes passing Puerto Rico. If these storms caused major damages to seagrass beds in the study area, seagrasses were able to recover quickly (two months for the 1950-1967 period and 4 years for the 1977-1993 period according to aerial photographs). This recovery is not consistent with previous observations of hurricanes impacts on seagrass beds in other geographic regions where seagrass beds may take years to recover (van Tussenbroek et al. 2014). Therefore, as suggested by Kendall et al. (2004), it is possible that hurricanes may have stimulated seagrass growth by pollination, seed dispersal, and vegetative propagation in Caja de Muertos, but this should be further analyzed.

The most striking finding, based on the NOAA hurricanes dataset, was the passage of tropical storm Baker directly over Caja de Muertos Island (Fig. 6) in August of 1950 (before the 1950 aerial photograph was taken). Given the trajectory of Baker and that another tropical storm (Isaac) passed further away from Caja de Muertos Island in 2012 causing significant damages to coastal ecosystems and infrastructure (ENDI, 2012), the seagrass increasing trend detected during 1950 and 1967 probably was a recovery response from damages caused by Baker. Results showed that increased seagrass after 1950 was mainly dominated by widely spaced patches of seagrass (patchy category, Fig. B.1), which characterizes the first step of the seagrass colonization process (Sintes, 2006).

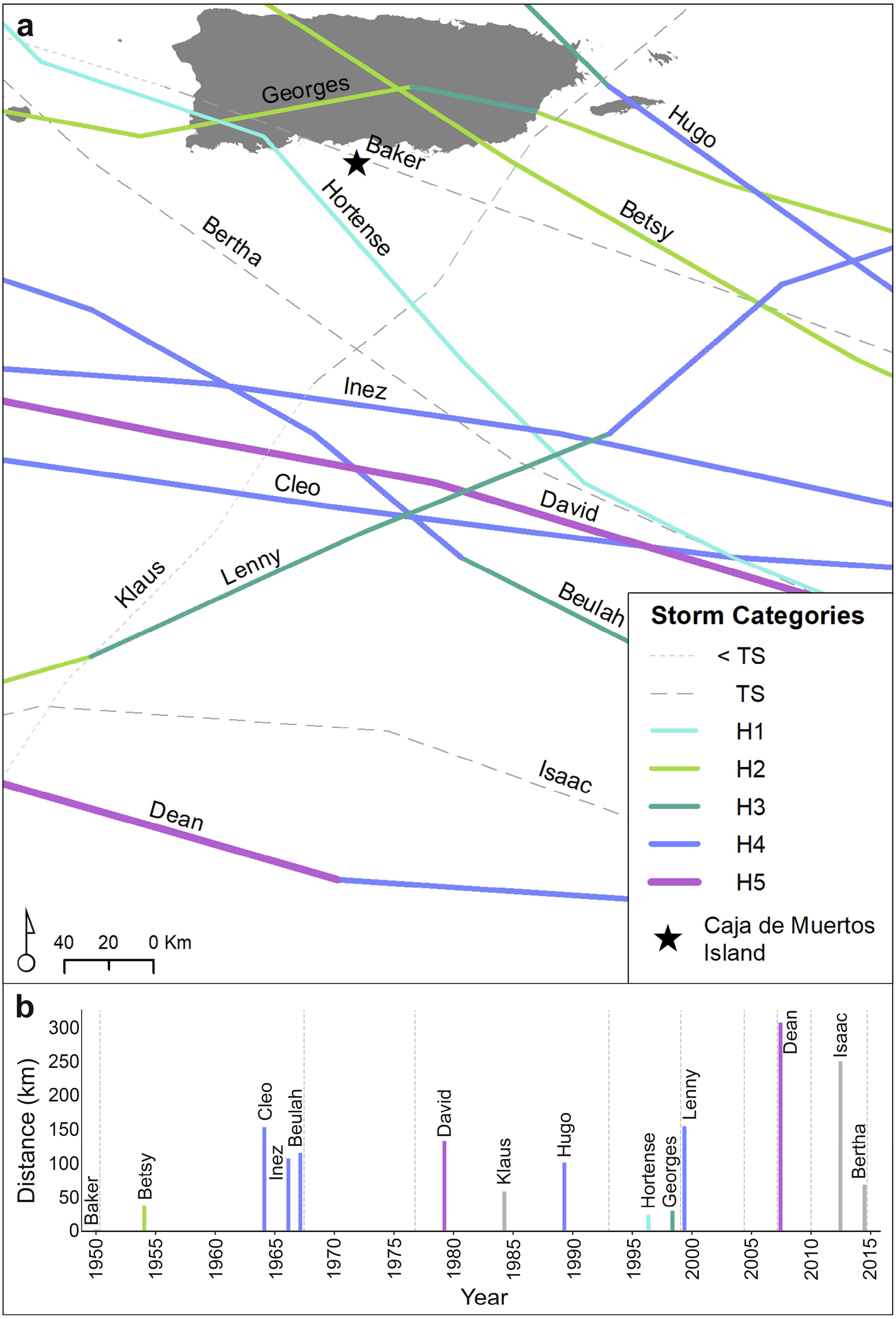
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Fig. 6 Historical tropical storms and hurricanes potentially affecting Caja de Muertos Island from 1950 to 2014 (NOAA, 2019) (a). Legend shows the storm category: TS (tropical storm), H1 to H5 (hurricane categories from 1 to 5). (b) Distance of storm from Caja de Muertos island. Dashed lines represent limits between different periods analyzed in this study. Selection of storm events was conducted considering the distance (~310 km) of the southernmost hurricane impacting seagrass in Caja de Muertos (R. Armstrong, Pers Comm.). Storm surge is greater in the right-front quadrat of the storm (NOAA, 2011), right of the landfall point (Rego and Li, 2010), and central mountain chain of Puerto Rico creates a shade effect for Caja de Muertos Island. This figure shows tropical storms and hurricanes passing South Caja de Muertos up to ~310 km. We did not include tropical storms that made landfall in Puerto Rico northeast of Caja de Muertos and tropical storms and hurricanes passing north of the central mountain chain of Puerto Rico.

A reduction in seagrass herbivory could have also played a key role in the seagrass expansion observed in Caja de Muertos. A factor that possibly contributed to the observed trends is the Caribbean-wide die-off of the long spine sea urchin, *Diadema antillarum* that occurred in 1983 (Lessios et al., 1984). Armstrong (1981) documented a seagrass extent decrease in La Parguera, Puerto Rico, between 1936 and 1951 and postulated that a population explosion of grazers (reef fishes and echinoids) could have been responsible for the observed decrease. Given that *D. antillarum* is an important herbivore in seagrasses (Creed et al., 2003; Gonzalez-Liboy, 1979; Ogden, 1976), its die-off could have caused the opposite effect in seagrass abundance. Further, *D. antillarum* populations are recovering slowly (Tuohy et al., 2020) and in the study area individuals were not observed 2015 (HJR Reefscaping, 2015; León-Pérez, 2016), neither in the last 15 years in a coral reef nearby Zones A and B (PRDNER, 2019). Besides urchins, sea turtle grazing can result in negative effects on seagrass aboveground biomass (Fourqurean et al., 2010; Heithaus et al., 2014; Molina-Hernandez and Tussenbroek, 2014). In Caja de Muertos Island, Vicente (2008) documented two areas (within Zone D) of intense grazing pressure by the green sea turtle, *Chelonia mydas*, but there is no data available to asses this species population trend in the study area that could reveal a reduction in grazing pressure.

Other alternative for the increase observed was the establishment of the CMINR in 1980. There is little support for this hypothesis given that an increase in seagrass extent was observed both before and after the establishment of the reserve. However, management strategies implemented after the establishment of the reserve (e.g. installation of mooring buoys) could have reduced stressors on seagrass beds, but this assumption must be further studied.

An input of nutrients coming from river discharges off the main island of Puerto Rico could be a contributing factor to the seagrass increase. Udy et al. (1999) in Australia correlated an increase in seagrass distribution and biomass with an increase in nutrient availability in the clear oligotrophic waters of Green Island, where light is not limiting seagrass growth, such as in Caja de Muertos Island (León-Pérez et al., 2019). In 2015, León-Pérez (2016) showed the presence of the algae *Chaetomorpha linum*, which is a nutrient indicator (Littler et al., 1989), but the presence of this algae could have been the result of nutrient inputs coming from the decomposition of pelagic *Sargassum* accumulated in the shoreline (H. Ruiz, Pers Comm.). Additional research is required to determine if an increase in nutrient availability is influencing seagrass cover in the study area.

Lastly, findings of our study showed an increasing trend in seagrass extent mainly driven by the patchy cover category, which may reflect processes of recovery from disturbances (Bell et al., 2006) or fragmentation from seagrass loss (Duarte et al., 2006). We suggest that patchy seagrass could emerged by the recolonization process after the impact of tropical storm Baker in 1950. However, other processes may have influenced the persistence of this seagrass cover category throughout the 64-years period analyzed. Dynamics of seagrass patches is linked to the magnitude and frequency of physical disturbances, such as hurricanes (Duarte et al., 2006). Therefore, tropical storms and hurricanes could have contributed to the current trends, where disturbances may have been enough to limit the progression to continuous seagrass cover. In localized areas, such as Zone D, grazing pressure could have also played a role (see discussion below).

4.2 Seagrass spatial and temporal variability

The seagrass persistence and variability maps highlighted spatial variations between zones, caused by differences in environmental, and potentially biological, characteristics of these habitats. Zone C showed the highest fluctuation and frequency of variability, meaning that seagrass cover changed the whole cover spectrum (e.g. no seagrass, patchy, and continuous) and that the changes were common during the studied period. León-Pérez et al. (2019) noted the presence of “blowouts” in Zone C, further confirming this seagrass bed is under frequent and notorious wave energy disturbances. We expect this patchy, high-energy seagrass bed to be more vulnerable to high wave energy events such as hurricanes (Fonseca et al., 2000).

Zone B showed the highest persistence of the continuous seagrass cover and the highest percentage of no variability, suggesting this seagrass bed may be at a steady state. Sintes et al.

(2006) indicated when seagrasses reach a steady state its clonal growth becomes slower and more compacted. At a steady state, an internal recolonization of gaps begins, and the growth of clones occurs primarily along the perimeter of the seagrass patch (Sintes et al., 2006). In Zone B, new seagrass areas occurred at the perimeter of this seagrass bed towards the coast (Fig. 3). Furthermore, Williams (1990) suggests that when *T. testudinum* community reaches its steady-state, niche partitioning may lead to the co-existence of more than one seagrass species. León-Pérez et al. (2019) found that continuous seagrass category in Zone B was composed of an intermixed community of *T. testudinum* and *S. filiforme*. Therefore, it is very likely that the seagrass bed in Zone B is in a steady state, which highlights the potential importance of it as a seed and asexual propagation source in the event of a major disturbance to seagrass habitats in Caja de Muertos Island.

Seagrass bed on Zone D is located within a reef lagoon delimited by a c-shaped shallow coral reef (León-Pérez et al., 2019). In this zone, more than half of seagrass bed persisted as patchy and showed a small percentage of seagrass areas with no variation. Seagrass variability possibly occurred as this seagrass bed expanded in the beginning of the time series (Fig. 4) towards all directions, then filling the internal sand gaps and surrounding the areas already colonized. This growth was restricted by the natural reef barrier that prevented further expansion of the seagrass bed (Fig. 3), a similar spatial growth behavior as observed in Bahia Salina del Sur, Vieques, Puerto Rico (Hernández-Cruz et al., 2006).

Persistence of the patchy seagrass cover in Zone D, it is not expected showing relation to strong wave energy disturbances since the surrounding coral reef protected the area from the incoming wave energy. This is probably why this was the only zone that did not experienced a marked decline in the period of 1993-1999. Another mechanism explaining this persistence is the intense grazing pressure of green sea turtles in this area (Vicente, 2008) that possibly limited the transition from a patchy cover to a continuous seagrass bed. Although its persistence as a patchy seagrass bed, this intermixed seagrass meadow (León-Pérez et al., 2019) seems to be less affected by wave energy due to its geomorphological characteristics. Similar to Zone B, in the event of a major disturbance it has the potential to provide seeds for the recolonization of nearby seagrass habitats in the island.

In Zone A, the patchy seagrass cover category largely dominated the area and only the continuous cover persisted in the deepest areas of the meadow (León-Pérez et al., 2019). Most of the area covered by this seagrass bed fluctuated in seagrass category: however, fluctuations were mainly low (LFIV and LFFV, Table 5) indicating that the changes were only between two seagrass cover categories, mainly no seagrass cover and patchy. Therefore, changes in this seagrass bed may occur and periods of no cover may happen normally as part of this seagrass bed ecological dynamics.

Ultimately, the seagrass persistence and variability maps (Fig. 5) provide a temporal baseline of seagrass cover for the study area by which potential future changes in seagrass category and their extent can be compared. Managers and researchers can use these maps to determine the severity of a natural or anthropogenic event within the studied zones in Caja de Muertos. For example, it may be considered atypical for Zone B to change to a patchy seagrass area, since Zone B has persisted as a continuous seagrass bed for 64 years, even after hurricanes. It could also be considered atypical for Zones A, C and D, if the seagrass in these areas disappeared or are further reduced. Thus, management concerns may arise if the continuous seagrass areas later turn to and persist as patchy or if patchy areas are further reduced.

4.3 Study limitations and future directions

The availability of a long-term aerial photography for Caja de Muertos Island represented a valuable historical record. Nevertheless, the potential sources of error in the analysis need to be considered. The photographs used were taken at different times of the year and it is known that seagrass meadows can experience seasonal variations (Green and Short, 2004). If indeed seasonal changes occurred in Caja de Muertos Island, such changes are expected to be small as seasonal variations in the tropics are less pronounced than in higher latitudes (Erftemeijer and Herman, 1994; Lanyon et al., 1995). On the other hand, another limitation of the study is the temporal scale that consisted on an aerial photograph each 3 to 17 years. This temporal scale may not be ideal for assessing, for example, the impacts of hurricanes on seagrass beds.

This study provides a long-term understanding of seagrass dynamics in Caja de Muertos Island. However, changes in the dynamics of seagrass cover at a finer temporal scale are still not well understood. In order to design effective conservation and management strategies, future research is needed to identify the underlying mechanisms, both natural and anthropogenic, that drive the observed changes (e.g. wave energy exposure and frequency, herbivores abundance, nutrient inputs, management strategies implemented), and to understand how these relate to inter- and intra- annual changes in seagrass cover category and extent. All of these will require the examination of seagrass beds at different ecologically meaningful scales of space and time.

Lastly, it is worth mentioning that time series in our study did not include 2017, when the category 4 Hurricane María impacted Puerto Rico significantly affecting marine ecosystems, including seagrasses (Hernández-Delgado et al., 2018; NOAA, 2018). Our preliminary examination of satellite data of Caja de Muertos Island from 2020 suggest a reduction in seagrass aerial extent after Hurricane María, including notorious declines in seagrass areas that persisted as continuous in Zone B. Consequently, our study provides the baseline information of long-term seagrass dynamics needed to assess the impacts of this event and therefore determine if management interventions are needed to ensure the long-term persistence of these seagrass habitats.

4 Conclusions

This study reconstructed the historical distribution of seagrass beds in Caja de Muertos Island, Puerto Rico, showing long-term changes in spatial distribution. There was a positive trend in seagrass cover with an overall increase of 64% from 1950 to 2014, driven by an increase in the patchy seagrass cover category. It is likely that seagrasses in Caja de Muertos were under a recovery phase after the impact of tropical storm Baker in 1950. Biological factors, such as the decrease in abundance of herbivores, could have also played a role in the observed increasing trend. On the other hand, Hurricanes Hortense and Georges seem to be related to the decrease in seagrass cover observed from 1993 to 1999. Variations in seagrass spatial cover were observed between zones, highlighting the localized effects of environmental conditions (e.g. wave energy exposure) and geomorphology on seagrass beds.

The imagery and methods used in our study prove to be effective for detecting trends and quantifying seagrass changes, which can be applied elsewhere to establish seagrass cover baselines by which future comparisons can be made. The seagrass persistence and variability maps created have the potential to be used by resource managers for assessing the severity of disturbances in seagrass beds and thereby determine if conservation strategies are needed.

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Supplemental Material

Appendix A

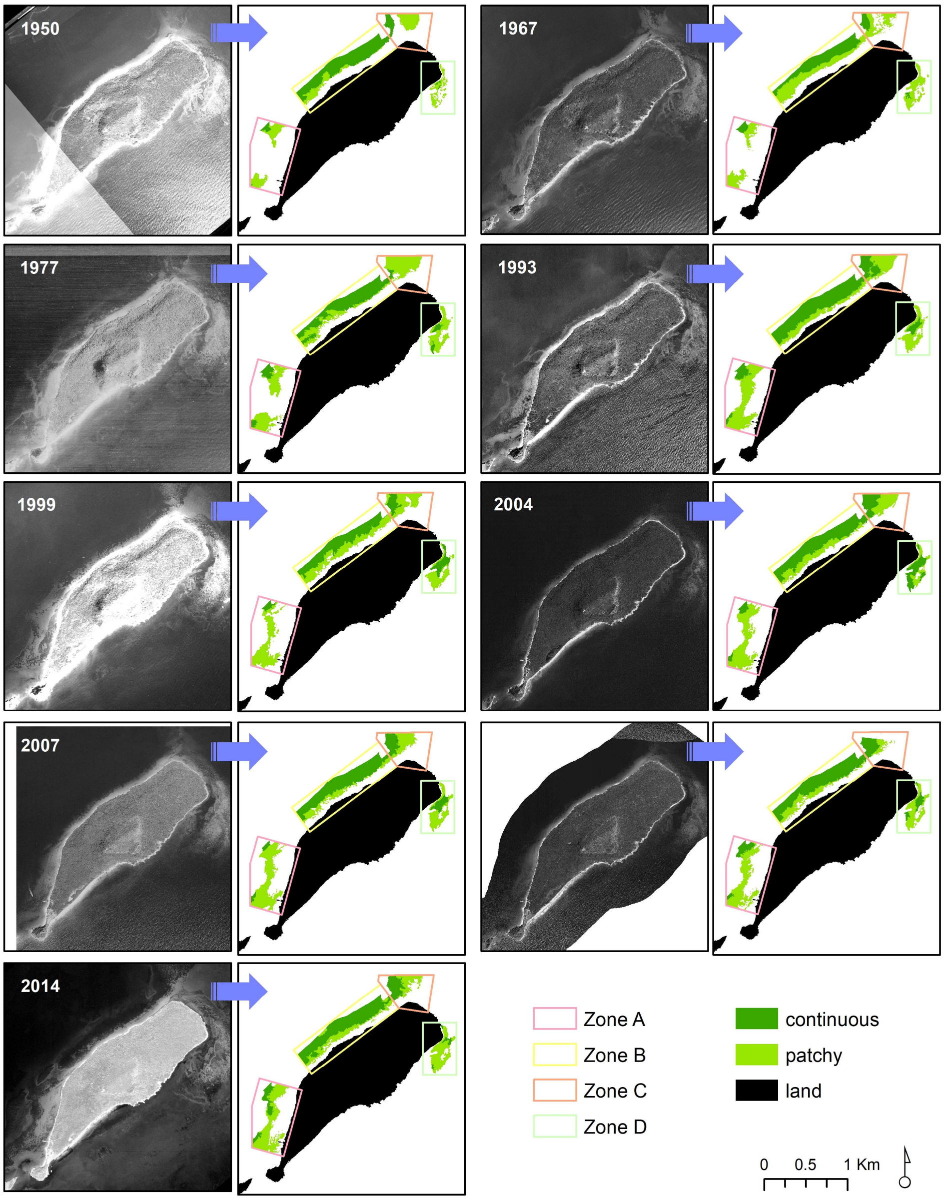

Fig. A.1 Raw panchromatic aerial photographs and WV-2 image of Caja de Muertos Island from 1950 to 2014, and the mapped seagrass extent (continuous and patchy cover categories) within the studied zones.

Appendix B

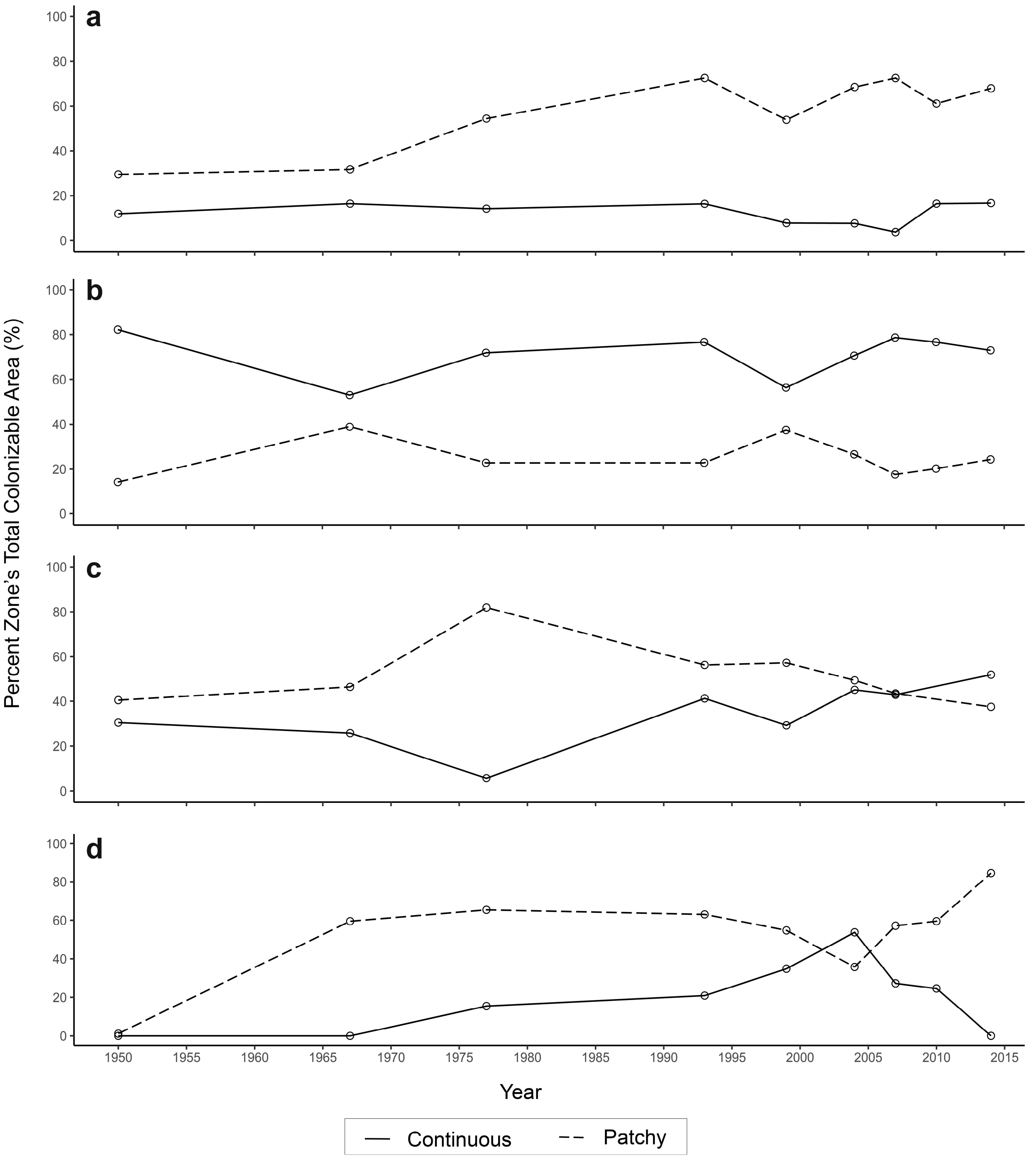

Fig. B.1 Continuous and patchy seagrass cover by zone between 1950-2014. Solid lines represent continuous zones and dashed lines represent patchy zones. Values represent the percentage of each seagrass cover category within each zone's total colonizable area.