Scientia Marina 86(2)
June 2022, e030, Barcelona (Spain)
ISSN-L: 0214-8358
https://doi.org/10.3989/scimar.05190.030

Communities of corals and crustose coralline algae of the Jardines de la Reina National Park, Cuba: global stressors and resilience (2001-2017)

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Summary: This study was conducted in the Jardines de la Reina National Park, Cuba. The health of the communities of corals and crustose coralline algae was studied in the years 2001, 2012 and 2017. The probable effect of hurricanes and sea surface temperature on these communities was also assessed. The area was only affected by three hurricanes and a tropical storm from 2000 to 2017. Sea surface temperature showed an increasing trend (by 0.03°C). The highest percentage of old mortality was recorded in 2001 (74% on the fore reef and 53% on reef crests) and the lowest of recent mortality in 2012 (0.03% on the fore reef and 0.17% on reef crests). Coral cover increased on the fore reef by between 3% and 2% in 2017 in comparison with 2001 and 2012. On the reef crests, the highest cover percentage was in 2001 (14.8%). Unlike local stressors, it was determined that hurricanes and sea surface temperature have likely negatively affected the coral reefs, particularly on reef crests. Both habitats have shown resistance and/or recovery capacity from the impacts suffered after 2001, which suggests some level of resilience.

Keywords: coral cover; coralline algae; hurricanes; temperature; Jardines de la Reina; Cuba.

Comunidades de corales y algas coralinas costrosas en el parque nacional Jardines de la Reina, Cuba: estresores globales y resiliencia (periodo 2001-2017)

Resumen: Este estudio se realizó en el Parque Nacional Jardines de la Reina, Cuba. Se estudió la salud de las comunidades de corales y algas coralinas costrosas en los años 2001, 2012 y 2017. También se evaluó el probable efecto de los huracanes y la temperatura superficial del mar sobre dichas comunidades. La zona solo ha sido afectada por tres huracanes y una tormenta tropical en este siglo (desde 2000 hasta 2017). La temperatura de la superficie del mar mostró una tendencia creciente (en 0.03°C). El mayor porcentaje de Mortalidad Antigua se registró en 2001 (74% en arrecife frontal y 53% en crestas del arrecife) y el más bajo de Mortalidad Reciente en 2012 (0.03% en arrecife frontal y 0.17% en crestas del arrecife). La cobertura de coral aumentó en el arrecife frontal en 2017, entre 3% y 2%, respecto de 2001 y 2012. En las crestas del arrecife, el mayor porcentaje de cobertura se registró en 2001 (14.8%). A diferencia de los factores de estrés locales, se determinó que los huracanes y la temperatura de la superficie del mar probablemente hayan afectado negativamente a los arrecifes de coral, particularmente a las crestas del arrecife. Ambos hábitats han mostrado resistencia y/o capacidad de recuperación de los impactos sufridos después de 2001, lo que sugiere cierto nivel de resiliencia.

Palabras clave: cobertura de coral; algas coralinas; huracanes; temperatura; Jardines de la Reina; Cuba.

Citation/Como citar este artículo: Hernández-Fernández L., Merino-Ibarra M., Matos Pupo F., González-De Zayas R. 2022. Communities of corals and crustose coralline algae of the Jardines de la Reina National Park, Cuba: global stressors and resilience (2001-2017). Sci. Mar. 86(2): e030. https://doi.org/10.3989/scimar.05190.030

Editor: E. Cebrián.

Received: April 22, 2021. **Accepted:** February 2, 2022. **Published:** June 2, 2022.

INTRODUCTION

Coral reefs are biodiverse and productive ecosystems, but they are threatened by local stressors, and by global stressors such as climate change (Hoegh-Guldberg et al. 2019, Gil-Agudelo et al. 2020). Global warming, overfishing, pollution and unregulated tourism have been determined as the biggest threats to coral reef (McLeod et al. 2013). Increasing pollution, overfishing and tourism are among the local stressors (Jackson et al. 2014), while the rise in the frequency and intensity of hurricanes (Webster et al. 2005) and in the sea surface temperature (SST) caused by global warming (Li and Reidenbach 2014) are among the effects of climate change. The response of coral reefs to these global stressors depends on the interaction between functional groups (Harborne et al. 2017) such as corals and macroalgae and the resilience capacity of each coral reef (Mumby et al. 2014).

The structure of Cuba's coral reef is quite variable. Unlike the ones located to the north of the mainland, reef ecosystems in the south are separated from the island by keys and large, deep lagoons with reef patches, which reduce the effect of global and local stressors on the health of these systems. Among the southern reefs, those of the Jardines de la Reina archipelago stand out particularly because of their conservation status (health) (González-Díaz et al. 2018). The Jardines de la Reina National Park (JRNP) is in this archipelago. This park is one of the most important marine protected areas of Cuba (Perera-Valderrama et al. 2018) and is regarded as the largest marine reserve in the Caribbean (Apeldoorn and Lindeman 2003).

In the JRNP, there are no indications to suggest that coral reefs are being affected by local stressors (González-Díaz et al. 2018, González-De Zayas et al. 2020). Although the park is used for tourist activities, particularly recreational diving, the reef communities of the diving sites are in good health (Hernández-Fernández et al. 2016a). Furthermore, the distance between the reef and the mainland prevents pollution from affecting the conservation status of these ecosystems. Other factors are the significant decrease in nutrient inputs to marine waters during the 1990s and the damming of rivers in Cuba. As a result of these conditions, the coral reefs of the JRNP have been regarded as oligotrophic (Baisre 2006). Nutrient levels in the waters of the park have remained homogeneous since the year 2000 (Hernández-Fernández et al. 2019a).

During the present century, the JRNP has been affected by four tropical cyclones, but studies have focused on the effects of only two of these storms (Pina-Amargós et al. 2008a, Guimarais et al. 2013). Increasing temperature has affected the coral reefs of the park, bringing about bleaching events (Hernández-Fernández et al. 2011). However, evidence of recovery of the coral reefs from these events has not been documented beyond that of the colonies that have recovered from the 2005 bleaching event (Hernández-Fernández et al. 2011). This recovery of coral reefs in the JRNP from 2005 bleaching events is an example of the resilience of corals, which showed their capacity to recover from disturbances such as increasing temperature (Gunderson 2000, Mumby et al. 2013). Two general attributes determine the response capacity of coral communities to temperature rise: (1) the sensitivity of individual corals and their record of exposure without bleaching, and their capacity to survive (resistance) in cases of bleaching; and (2) the recovery potential related to the capacity of the community to retain or recover its structure and functioning in spite of coral mortality (resilience) (Obura and Grimsdith 2009).

No comprehensive study of the effects of global stressors on the coral reef of the JRNP and their potential resilience has been published. Undoubtedly, research on coral reefs distant from human settlements, such as those of the JRNP, provides a unique opportunity to determine how resilient these ecosystems are to climate change, a phenomenon that is already causing probably irreversible damage to them (Rey-Villiers et al. 2016). The hypothesis of this study is that unlike local stressors, hurricanes and global warming (global stressors) have affected the coral reef of the JRNP, but it has been resilient thanks to a great resistance and/or recovery capacity. For this reason, the objective of this work is to study the possible effect of global stressors (hurricanes and increasing SST) on the health of corals and crustose coralline algae (CCA) on the reef crests and fore reef of the JRNP during the period 2001-2017.

MATERIALS AND METHODS

The Jardines de la Reina archipelago (21°21'16''N 79°75'5''W–20°87'16''N 78°54'66''W) is formed by 661 keys and islands and extends along 360 km, paralleling the southern coast of the Cuban provinces of Camaguey, Ciego de Ávila and Sancti-Spiritus. The waters of the Gulf of Ana María are to the northwest of the archipelago and those of the Caribbean Sea to the south. In 1996, the Cuban Ministry of Fisheries proclaimed approximately 950 km^2 of the archipelago a "zone under special regime of use and protection". This management category is equivalent to the internationally recognized Marine Reserve. The entire area, from Cayo Breton to Cayo Cabeza del Este, was established as a National Park in 2010 on account of its ecological values and conservation status, according to the Cuban Council of Ministers.

Based on the experience gathered from over 15 years of work in the study area, and on research done between 2008 and 2019 (Pina-Amargós et al. 2008b, 2014, Hernández-Fernández et al. 2019b), a gradient with a higher level of protection in the central portion of the JRNP was established. Because this gradient decreases towards the limits of the reserve, the study sites for surveying fore reef habitats were located in five reserve zones: the Westernmost Reserve, the Western Reserve, the Central Reserve, the Eastern Reserve and the Easternmost Reserve. The sites for studying the reef crests were located in only three zones: the Central Reserve,

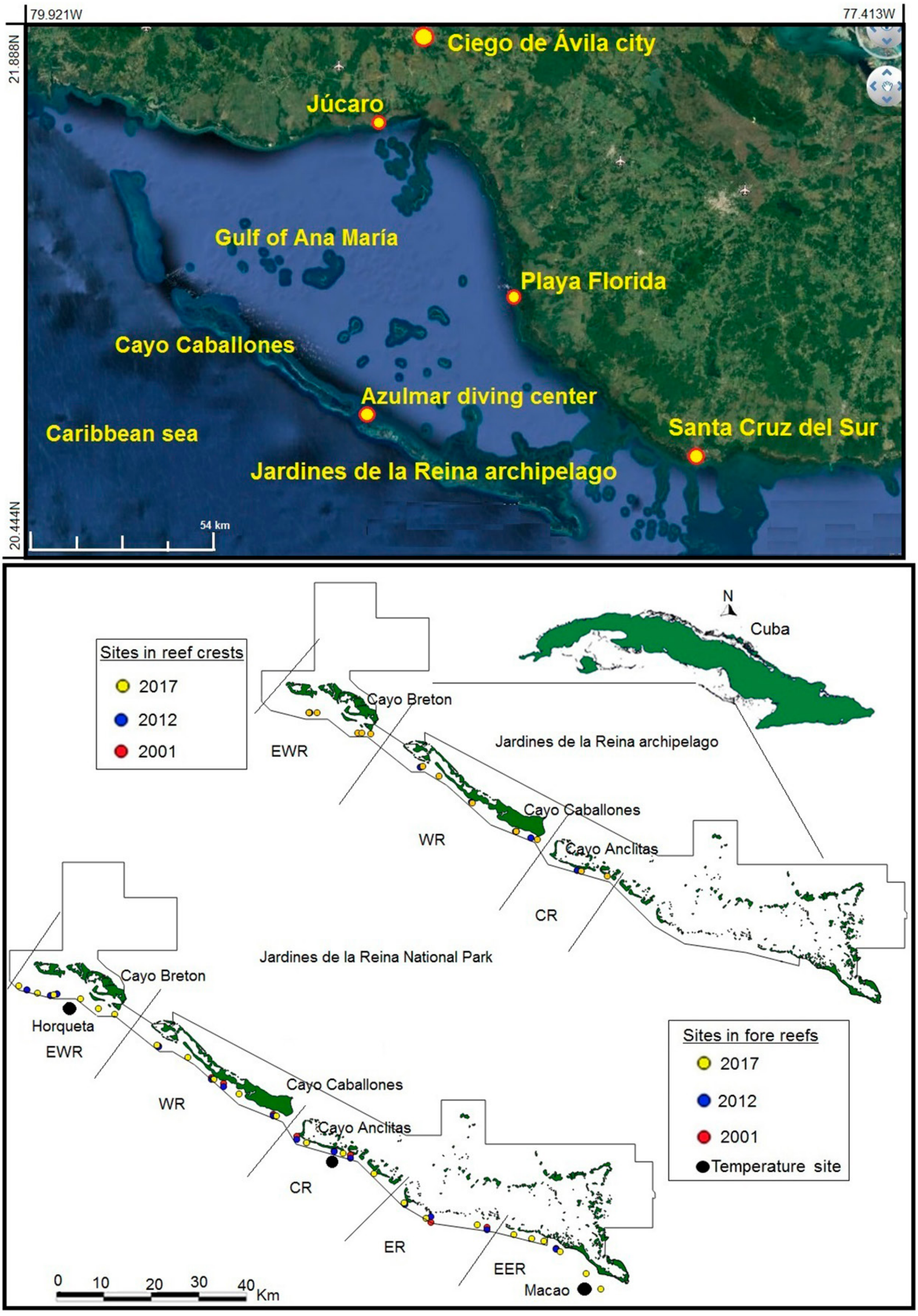

Fig. 1. – Study area. Sampling sites per year. Zones of the JRNP (EWR, Westernmost Reserve; WR, Western Reserve; CR, Central Reserve; ER, Eastern Reserve and EER, Easternmost Reserve). Horqueta, Anclitas and Macao: sites where average monthly temperature was measured.

the Western Reserve and the Westernmost Reserve. In the eastern area there are no typical reef crest formations (Hernández-Fernández et al. 2019c) (Fig. 1).

To determine the effects of tropical cyclones on the JRNP, historic chronology (from 1851 to 2017) was considered, using the database from the Institute of Meteorology of Cuba and published papers on tropical cyclones (Pérez 2013 and Córdova-García et al. 2018).

Three sites, Horqueta (21°06'6"N 79°41'71"W), Anclitas (20°78'6"N 78°93'81"W) and Macao (20°53'975"N 78°40'88"W), were chosen to document SST variations in the JRNP (Fig. 1). These sites were selected because 1) coral reef monitoring were available for each site and 2) they are situated at the extremes and centre of study area. Average monthly temperature from 2003 to 2017 was obtained using satellite image (MODIS satellite) and the temperature database of the National Oceanic and Atmospheric Administration at the website https://worldview.earthdata.nasa.gov. The MODIS L3 SST 4 km layer shows global daytime SST at a depth of a few micrometres with ranges from –1.8°C to 32°C (Fig. 1).

To assess normality, data were processed using the Shapiro-Wilk and Bartlett tests. For data that did not meet normality standards, the nonparametric Kruskal-Wallis test was used. Temperature trend analysis was performed using the Mann-Kendall test. All statistical analyses were performed using the XLSTAT Program Version 2016.02.28451.

Reef crests (1-3 m deep) and fore reef (8-15 m deep) (Fig. 1) located south of the cays were studied in August 2001, April 2012 and September 2017. The linear transect method was used for the sampling units (10 m length), randomly extended over the sea bottom. For each coral under a transect (at least 10 cm wide), the indicators old mortality (OM) (%), recent mortality (RM) (%) and live coral cover (%) were described. To quantify the coral recruit density (colonies m^{-2}) and CCA (%), we used a PVC square sampling frame (25×25cm) deployed within the coral transect (4 per transect in 2001; between 1 and 3 per transect and 5 per transect in 2017) (Table 1). All samplings were performed according to methodologies proposed by AGRRA (2000) and the simplified version of AGRRA (2000) (Caballero et al. 2013). Fourteen fore reefs and six reef crests were surveyed in 2001 and 2012, and 24 fore reefs and 15 reef crests were surveyed in 2017. The sites were arranged by reserve zones (Table 1). The term "corals" includes the organisms contained in the order Scleractinia and the genus *Millepora* of the order Capitata.

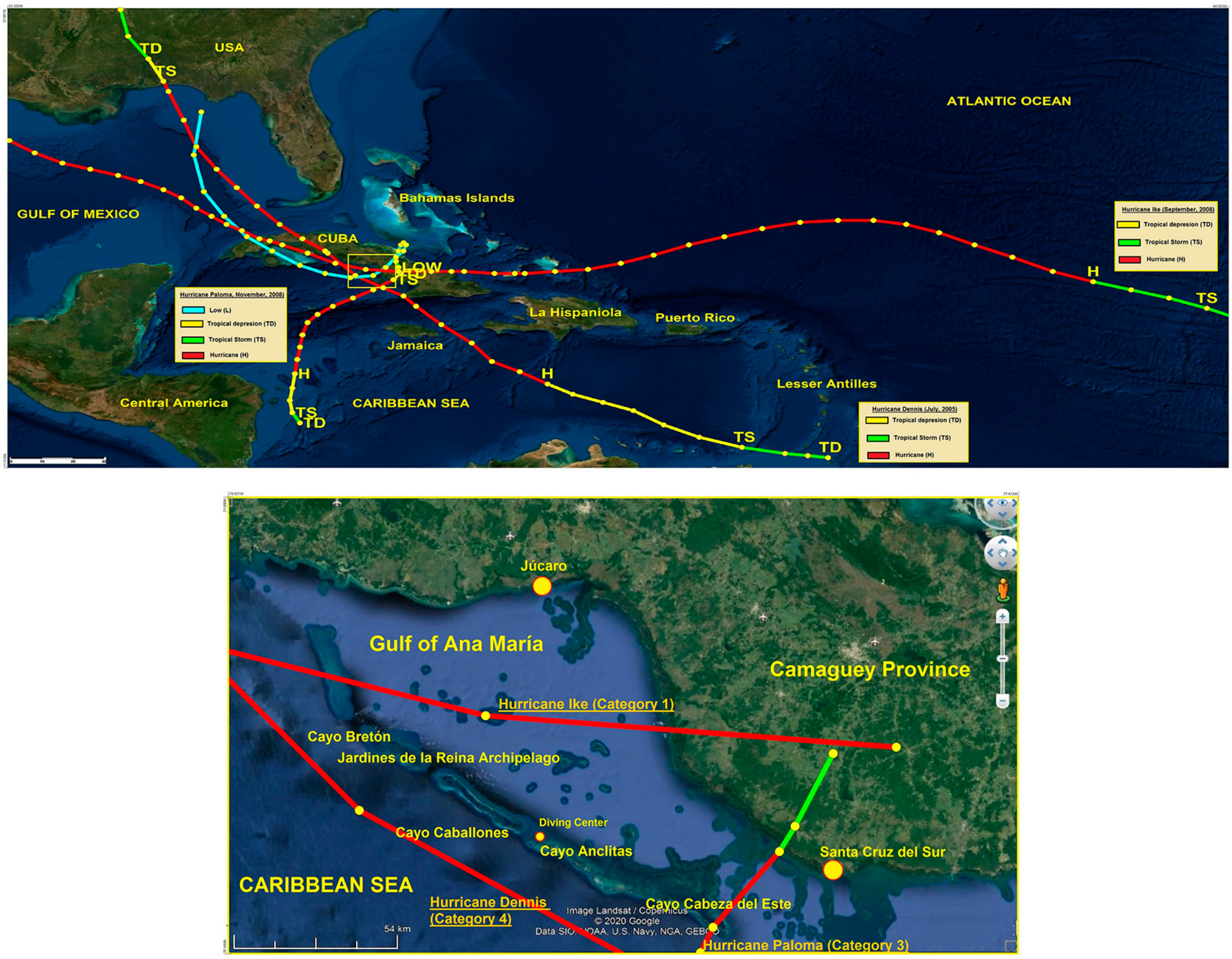

Fig. 2. – Hurricanes that affected the JRNP from 2000 to 2017.

Table 1. – Number of quadrats used to study crustose coralline algae and number of transects used for corals. Number of coral colonies per reserve zone on the reef crests and fore reefs. Reserve xones: EWR, Westernmost Reserve; WR, Western Reserve; CR, Central Reserve; ER, Eastern Reserve; EER, Easternmost Reserve.

Reserve zones	Years	Quadrats	Transects	Coral colonies
Fore reefs				
EER	2001	28	6	75
ER	2001	78	18	213
CR	2001	94	22	271
WR	2001	112	24	359
EWR	2001	81	18	212
EER	2012	24	8	64
ER	2012	57	38	415
CR	2012	81	46	522
WR	2012	72	45	430
EWR	2012	81	48	452
EER	2017	298	60	792
ER	2017	150	30	445
CR	2017	200	40	690
WR	2017	250	50	846
EWR	2017	268	60	718
Reef crests				
Reserve zones	Years	Quadrats	Transects	Coral colonies
CR	2001	47	12	78
WR	2001	78	20	191
EWR	2001	25	7	77
CR	2012	54	31	179
WR	2012	78	49	222
EWR	2012	27	16	57
CR	2017	199	39	300
WR	2017	250	50	336
EWR	2017	300	60	417

To know the historical status of the coral reef of the JRNP and whether it is resilient, health indicators between years (2001, 2012 and 2017) and between reserves per zone year were compared. These ecological indicators (OM, RM, live coral cover, coral recruit density and CCA cover) were selected taking into account that coral mortality could be a consequence of ocean warming and other climate events, such as the increasing number and frequency of strong hurricanes (Steneck et al. 2019). One aspect of climate variability is increasing SST, which could be related to coral cover variability (Soto et al. 2011). Williams et al. (2014) found that increasing SST negatively affected CCA cover, which is important for coral larval settlement (Adey 1998).

To assess normality, the data (OM, RM, live coral cover, recruit density and CCA cover) were processed using the Shapiro-Wilk W and Bartlett tests. The data did not meet normality standards, so the nonparametric Kruskal-Wallis test was used. When significant differences were documented, the Wilcoxon test was used to determine the elements showing the differences. For normal results, ANOVA was used (mean monthly SST). Statistical analyses were carried out with the R software version 3.1.2 (R Core Team 2014), vegan package (Oksanen et al. 2014).

RESULTS

Hurricanes

The area was only affected by three hurricanes and a tropical storm from 2000 to 2017 (Table 2, Fig. 2). During the 149 years before 2000 (1851-1999), four major hurricanes (categories 3-5 according to the Saffir-Simpson Wind Scale) impacted the province of Ciego de Ávila. However, only one of those hurricanes hit the JRNP. In 1932, a major hurricane (category 4) known as the Hurricane of Santa Cruz del Sur hit the area on 9 November 1932. Maximum sustained winds were close to 240 km h^{-1}.

Table 2. – Tropical cyclones that have affected the JRNP in the present century (2000-2017).

Tropical cyclone	Year	Category	Date
Dennis	2005	Hurricane, Category 4	8 July
Fay	2008	Tropical Storm	17 August
Ike	2008	Hurricane, Category 1	8 September
Paloma	2008	Hurricane, Category 3	8 November

Sea surface temperature

Monthly mean SST was studied at three sites of the JRNP, but no significant differences between sites were found. The mean SST value for the whole study area (using the SST of the three sites) was used for every statistical analysis. Mean SST had a value of 28.69±1.59°C during the period studied (2003-2017). Significant differences of annual mean SST between years were not found ($p>0.05$) (Fig. 3A). However, in some years (2003, 2013, 2014, 2015, 2016 and 2017) mean SST was above the mean value of the period. The highest mean values were recorded in 2015 (29.21±1.60°C) and 2016 (29.03±1.47°C) (Fig.3A), coinciding with a very strong El Niño Event. SST showed a significant tendency to increase ($\tau=0.70$, p-value<0.005), rising by 0.03°C between 2003 and 2017 (Fig. 3B).

Mean monthly SST showed a rather seasonal behaviour; January, February and March (the cold, dry season) showed no differences, and July, August and October (the warm, wet season) showed similar values. The highest monthly mean SSTs were in September (31.01±0.44°C) and August (30.50±0.43°C) (Fig. 4). Although in 2015 both months had the highest temperature for the whole study period (31.6°C and 31.5°C, respectively), these values showed no significant differences from the mean temperature in the same months in other years.

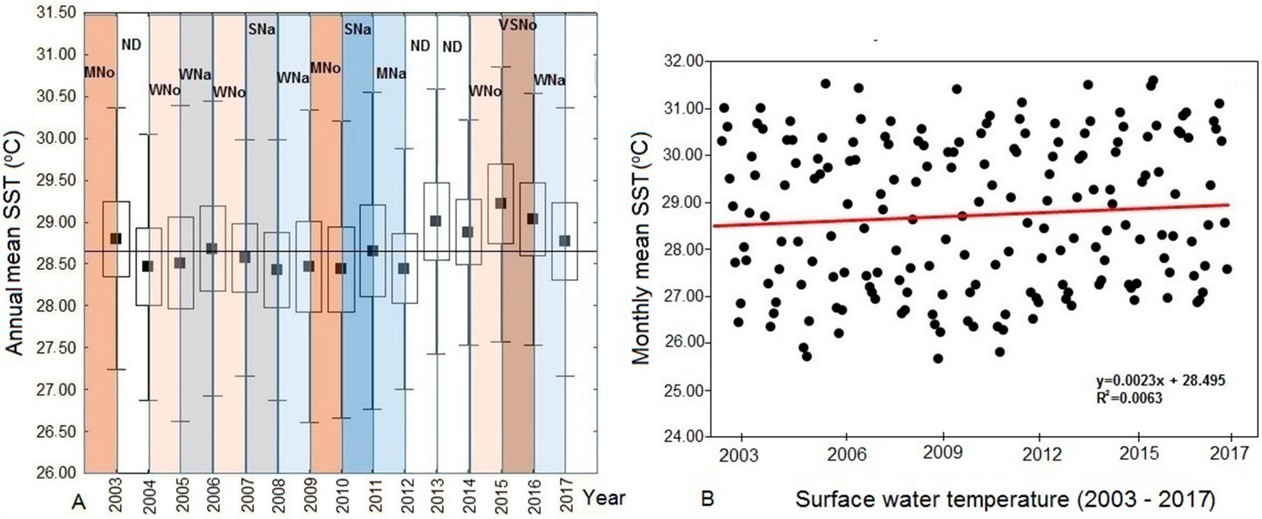

Fig. 3. – Annual mean SST (A) and SST tendency (B) for the 2003-2017 period. A. The horizontal black line shows annual mean value and coloured vertical bars show incidence of El Niño and La Niña events. WNo (Weak Niño); MNo (Moderate Niño); VSNo (Very Strong Niño); WNa (Weak Niña); MNa (Moderate Niña); SNa (Strong Niña); ND (No data). The boxes represent mean±SE and the vertical bars represent mean±SD. B. The red line represents temperature tendency.

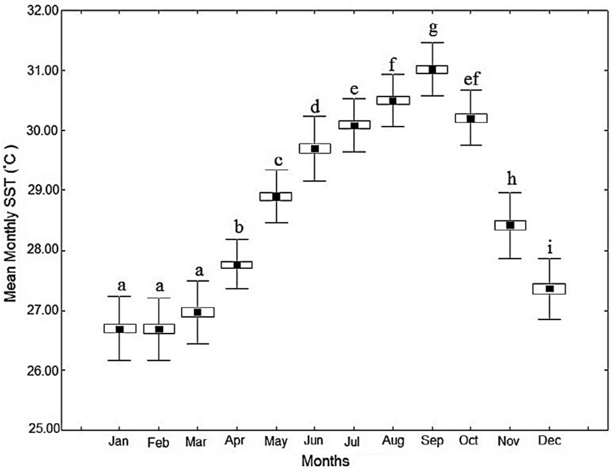

Fig. 4. – Monthly mean SST (°C) for the 2003-2017 period. The boxes represent mean±SE and the vertical bars represent mean±SD. The letters represent the differences recorded.

Ecological indicators

OM showed significant differences between the years surveyed on the fore reef and on the reef crests (Fig. 5A, B). In both habitats, the highest percentage of OM occurred in 2001: 74% on the fore reef and 53% on the reef crests. OM on the fore reef and reef crests decreased in 2012 (by 12.5% on the fore reef and by 21% on the reef crests) and it increased in 2017 (by 17.4% on the fore reef and by 22.4% on the reef crests) (Fig. 5A, B). OM showed no significant differences between zones of reserve on the fore reef in 2001 and 2012, but significant differences in 2017 (Fig. 6A). On the reef crests, differences were observed in 2001 (Fig. 6B).

RM showed significant differences between the years surveyed on the fore reef in 2001 (3.1%), 2012 (0.03%) and 2017 (2.7%) and on the reef crests in 2001 (3.6%), 2012 (0.17%) and 2017 (7%) (Fig. 5A, B). Significant differences between zones of reserve were only recorded on fore reef in 2017 (Fig. 6A, B).

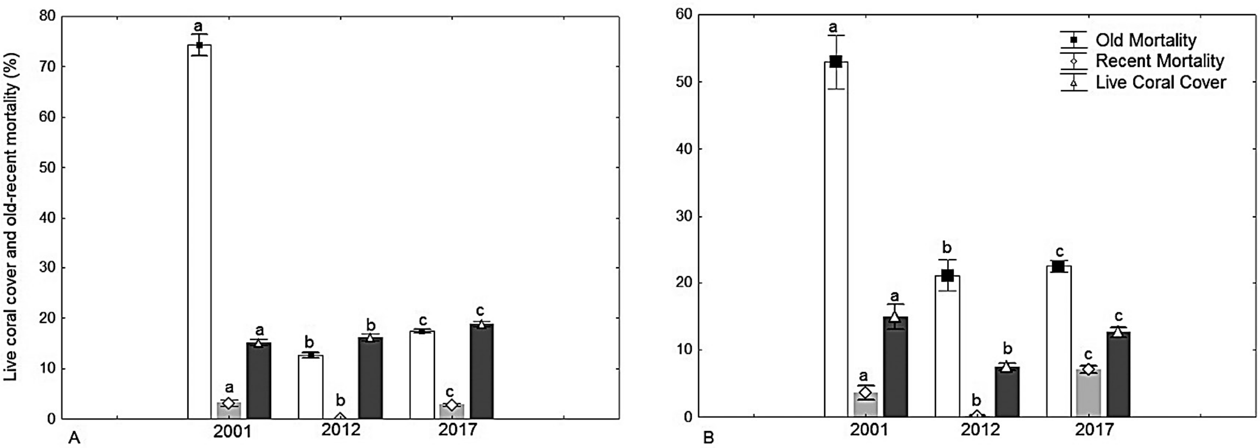

Fig. 5. – Old mortality (OM), recent mortality (RM) and live coral cover (%) on the fore reef (A) and reef crests (B) in 2001, 2012 and 2017. A: OM (df=2, p-value <2.2e-16), RM (df=2, p-value <2.2e-16), live coral cover (df=2, p-value=9.802e-06). B: OM (df=2, p-value=2.058e-12), RM (df=2, p-value <2.2e-16), live coral cover (df=2, p-value=5.169e-07).

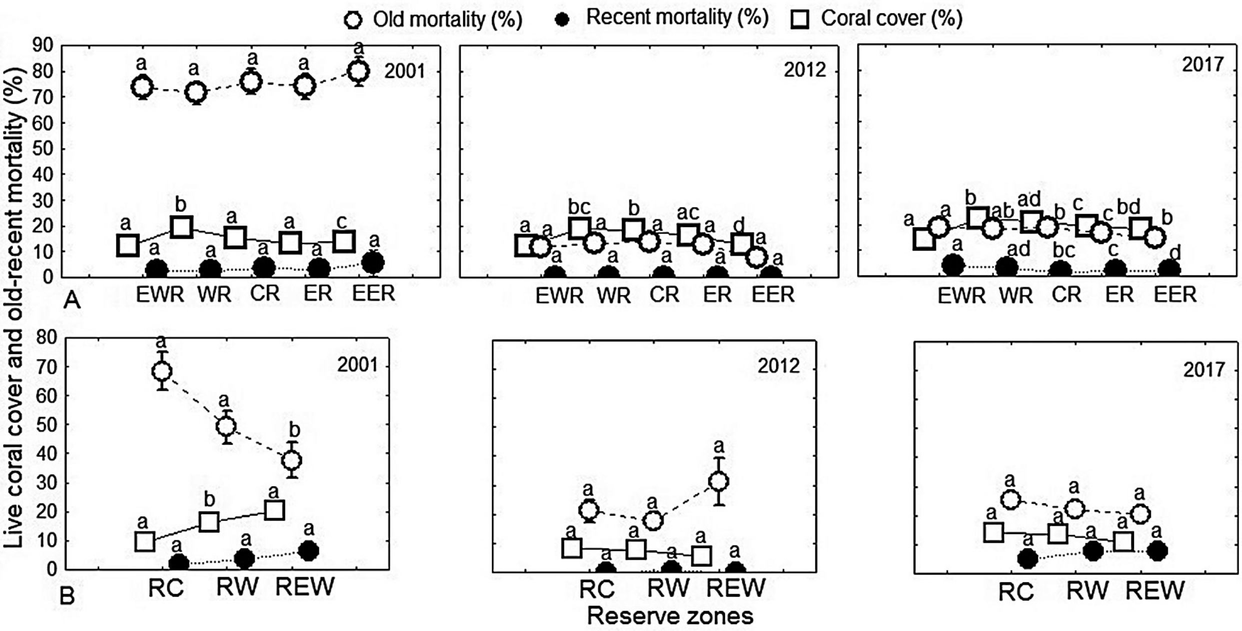

Fig. 6. – Coral cover, old mortality and recent mortality (%) on the fore reef (A) and reef crests (B) (EWR, Westernmost Reserve; WR, Western Reserve; CZ, Central Reserve; ER, Eastern Reserve and EER, Easternmost Reserve). **A. 2001:** OM (df=4, p-value=0.9054), RM (df=4, p-value=0.9718), live coral cover (df=4, p-value=0.01521). **2012:** OM (df=4, p-value=0.2007), RM (df=4, p-value=0.3133), live coral cover (df=4, p-value=3.554e-05). **2017:** OM: (df=4, p-value=0.001946), RM (df=4, p-value=0.007323), live coral cover (df=4, p-value=9.758e-09). **B. 2001:** OM (df=2, p-value=0.02283), RM (df=2, p-value=0.1038), live coral cover (df=2, p-value=0.07346). **2012:** OM (, df=2, p-value=0.5809), RM (df=2, p-value=0.619), live coral cover (df=2, p-value=0.05107). **2017:** OM (df=2, p-value=0.2334), RM (df=2, p-value=0.06301), live coral cover (df=2, p-value=0.3844).

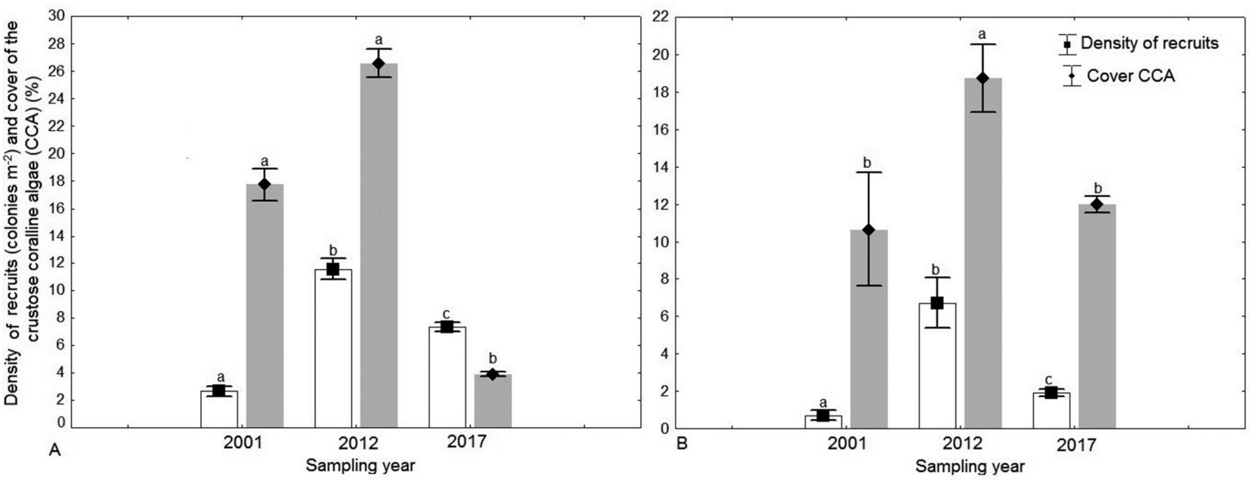

Fig. 7. – Recruit density (colonies m^{-2}) and cover of crustose coralline algae on the fore reef (A) and reef crests (B) in 2001, 2012 and 2017. A, recruit (df=2, p-value=5.578e-07), cover (df=2, p-value < 2.2e-16). B, recruit (df=2, p-value=0.000634), cover (df=2, p-value=0.00712).

On the fore reef and reef crests, coral cover showed significant differences between the three years surveyed. On the fore reefs, the lowest coral cover was in 2001 (15.2%), followed by 2012 (16.2%), and the highest in 2017 (18.8%) (Fig. 5A). On the reef crests, the highest coral cover was in 2001 (14.8%). Coral cover decreased to 7.4% in 2012 and increased to 12% in 2017 (Fig. 5B). On the fore reefs, the coral cover showed significant differences between zones of reserve in the three sampling years (Fig. 6A), while on the reef crests significant differences were only recorded in 2001 (Fig. 6B).

The highest recruit density on the fore reef was recorded in 2012 (11.2 colonies m^{-2}), followed by 2017 (7.7 colonies m^{-2}) and 2001 (2.6 colonies m^{-2}) (Fig. 7A). Recruit density on the reef crests showed significant differences between the three sampling years, with the highest density in 2012 (6.7 colonies m^{-2}), followed by 2017 (1.9 colonies m^{-2}) and 2001 (0.7 colonies m^{-2}) (Fig. 7B). Between zones of reserve, recruit density showed significant differences on the fore reefs in 2017 and on the reef crests in 2001 (Fig. 8A, B).

CCA cover was significantly different in the years 2001 (18%) and 2012 (26.5%) in comparison with 2017

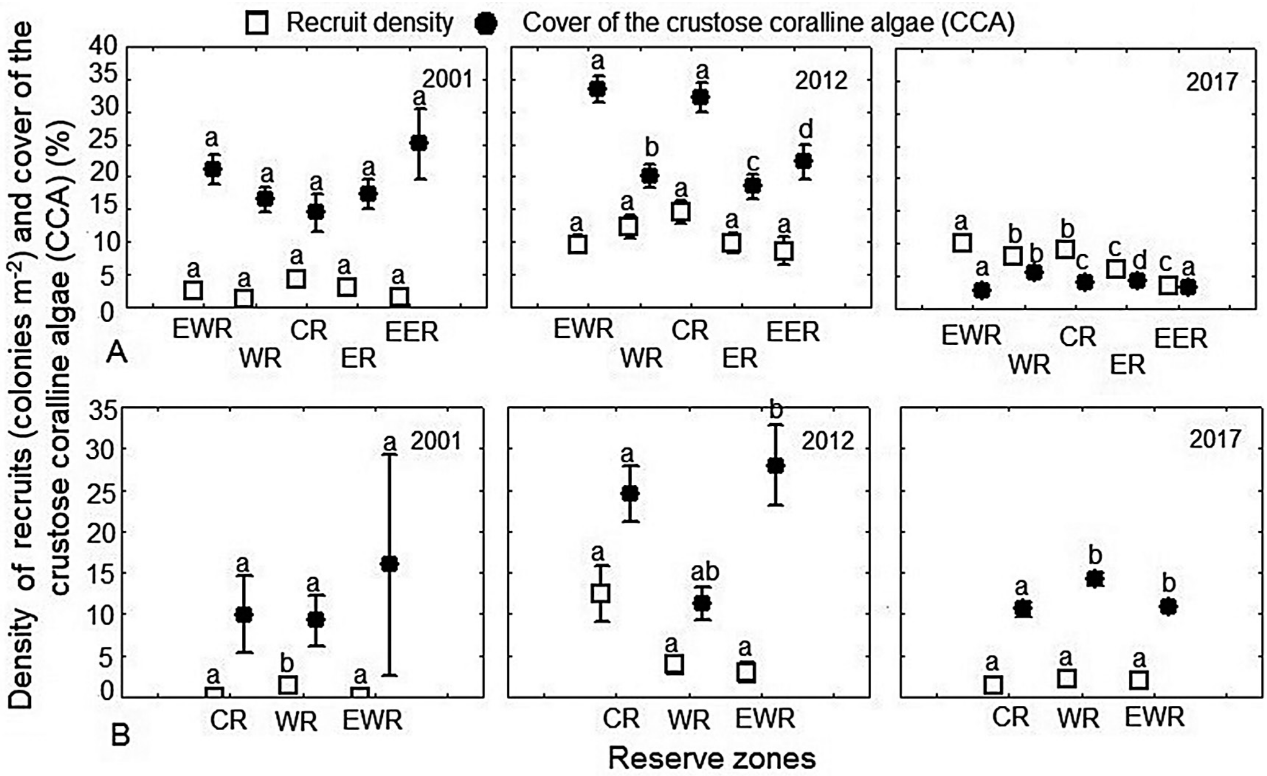

Fig. 8. – Recruit density (colonies m^{-2}) and cover of crustose coralline algae on the fore reef (A) and reef crests (B) (EWR, Westernmost Reserve; WR, Western Reserve; CZ, Central Reserve; ER, Eastern Reserve and EER, Easternmost Reserve). **A. 2001:** recruit (df=4, p-value=0.05659), cover (df= 4, p-value=0.06401). **2012:** recruit (df=4, p-value=0.3086), cover (df=4, p-value=3.173e-09). **2017:** recruit (df=4, p-value=1.668e-12), cover (df=4, p-value=3.232e-06). **B. 2001:** recruit (df=2, p-value=0.02439), cover (df=2, p-value=0.6849). **2012:** recruit (df=2, p-value=0.09995), cover (df=2, p-value=1.302e-06). **2017:** recruit (df=2, p-value=0.2069), cover (df=2, p-value=0.0006412).

(4%) on the fore reefs, and in the years 2001 (10.6%) and 2017 (12%) in comparison with 2012 (18.7%) on the reef crests (Fig. 7A, B). Between zones of reserve, CCA cover showed no significant differences in 2001 on either the fore reefs or the reef crests (Fig. 8A, B).

DISCUSSION

Several studies on coral reefs suggest that the decline of this ecosystem is caused by climate-induced stress resulting from events such as El Niño and intense hurricanes (Lirman et al. 2013, Hughes et al. 2017, Steneck et al. 2019). Consequently, long-term predictions regarding the status of coral reefs are not favourable. However, human beings can help mitigate the decline of these already damaged ecosystems through local management actions, which help to enhance the conditions for regeneration and growth of coral recruits. These management actions could help increase coral resilience (Steneck et al. 2019).

The JRNP is a good place for studying the resistance and recovery of coral communities to climate change. In this marine protected area (MPA) there is no evidence of a negative impact from local stressors on the reef of the park (González-Díaz et al. 2018, González-De Zayas et al. 2020), in spite of tourist activities such as recreational diving (Hernández-Fernández et al. 2016a) and pollution sources (towns, rivers and runoff from mainland) (Hernández-Fernández et al. 2019a). In the 1980s, a bleaching event took place in the Caribbean region and in 1998, a severe El Niño event caused major damage at a much larger scale, affecting coral reefs (Edmunds 2017). In Cuba, the coral reef also suffered massive mortality between the years 1987 and 1992 (Claro 2007). According to Hernández-Fernández et al. (2019a), algae dominance and low coral cover in the JRNP were probably caused by effects of global climatic changes on the coral community.

In the JRNP, annual average SST showed no significant differences between the 14 years surveyed. However, SST increased by 0.03°C in the entire period. This behaviour must be monitored because, according to Bruno et al. (2018), SSTs within MPAs are projected to increase by 0.035°C per year. For Cuban coastal waters, Planos et al. (2012) concluded that, around Cuba, SST increased by 1.0°C between 1966 and 2000, and this increase was highest on the occidental coasts of the country. Glenn et al. (2015) found a regional increase in SST of 0.015°C per year (greater than our results) for the period 1982-2012 in the Caribbean Region, but Muñiz-Castillo et al. (2019) reported that in the Caribbean there were differences in SST variability between regions (including our study site) and concluded that local-scale variability in oceanographic conditions such as depth, upwelling, currents and water circulation also influences heat stress patterns at the local scale. There were SST variations in the JRNP (up to 5.0°C) from one month (or group of months) to another. Such

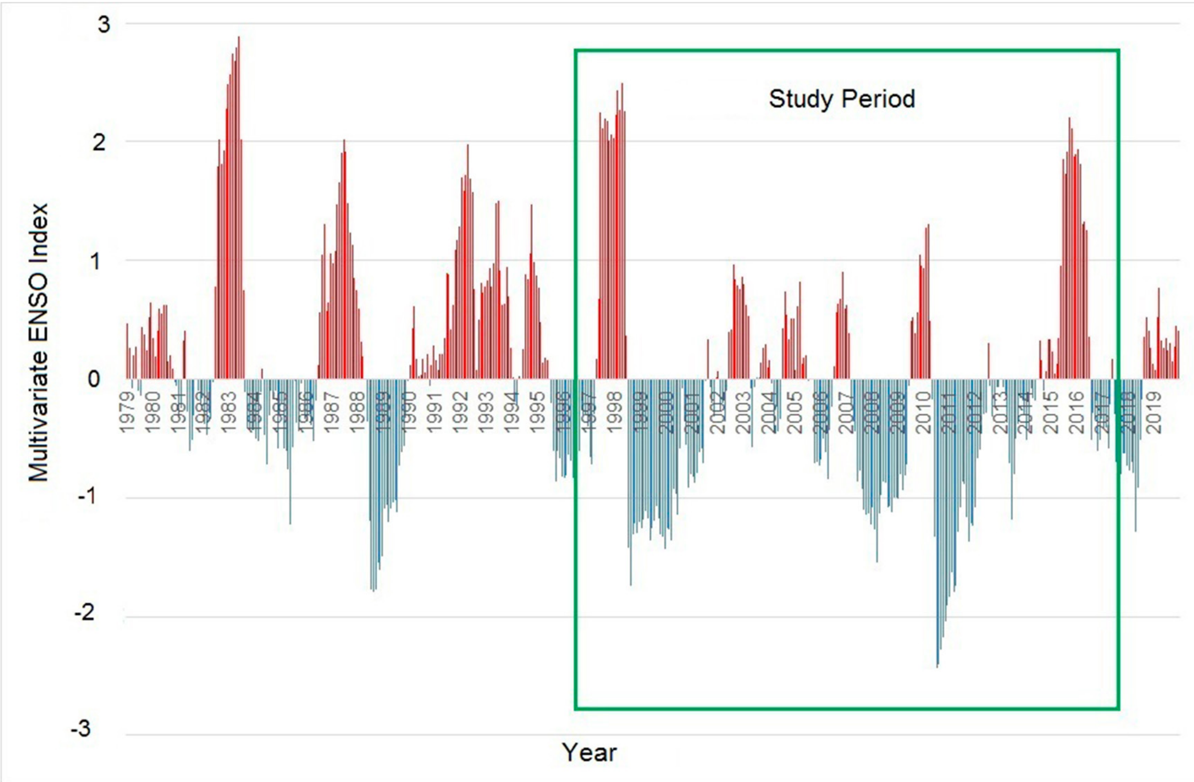

Fig. 9. – Period of study of El Niño and La Niña events. Red bars, Niño; Blue bars, Niña.

Table 3. – Years and intensity of El Niño and La Niña. Based on Oceanic Niño Index. Jan Null, CCM. Updated in Dec.-Jan.-Feb. 2020. https://ggweather.com/enso/oni.htm

El Niño	La Niña					
Weak-10	Moderate-7	Strong-5	Very Strong-3	Weak-10	Moderate-4	Strong-7
1952-53	1951-52	1957-58	1982-83	1954-55	1955-56	1973-74
1953-54	1963-64	1965-66	**1997-98**	1964-65	1970-71	1975-76
1958-59	1968-69	1972-73	**2015-16**	1971-72	1995-96	1988-89
1969-70	1986-87	1987-88		1974-75	**2011-12**	**1998-99**
1976-77	1994-95	1991-92		1983-84		**1999-00**
1977-78	**2002-03**			1984-85		**2007-08**
1979-80	**2009-10**			**2000-01**		**2010-11**
2004-05				**2005-06**		
2006-07				**2008-09**		
2014-15				**2016-17**		

variations were more evident between the rainy and dry seasons. This SST range of variation could favour coral resilience in the JRNP. According to Soto et al. (2011), corals under moderate temperature variations are more resilient than those under low variability or extreme temperatures, as a result of their exposure and acclimatization to greater temperature variability.

All climatic and oceanographic variables (SST, rain and storm frequency anomalies) resulting from El Niño and La Niña events could have influenced the behaviour of coral communities in the JRNP. The OM percentage was higher in 2001, which could have resulted from the severe 1998 El Niño event (Table 3, Fig. 9) (Muñiz-Castillo et al. 2019). The period 1998-2000 was precisely the first heat-related stress period that coincided with the Oceanic Niño Index. A strong El Niño event took place in 1997-1998 (Table 3), although it was followed by a La Niña event in 1999-2000 (Table 3, Fig. 9) (Muñiz-Castillo et al. 2019).

Not only El Niño events could be the cause of high OM in the JRNP in 2001; a period of 73 years without hurricanes (from the Hurricane of Santa Cruz del Sur in 1932 to Hurricane Dennis in 2005), could be another cause. Hurricane frequency in the JRNP is regarded as low, taking into account that the area has only been affected by three hurricanes and a tropical storm in this century. Although hurricanes are largely deemed as destructive and catastrophic events, they can also benefit tropical and subtropical marine ecosystems, because they absorb energy from surface waters through transference of latent heat, thus reducing SST. They can also bring to the surface cooler deep waters, which together with their cloud systems lower surface temperatures. This cooling process depends on the characteristics of the hurricane and of depth-related temperature variations at each site (Heron et al. 2008).

Bleaching and sea temperature rise are two of the most serious and imminent threats to coral reef (Obura and Grimsdith 2009, Hughes et al. 2017), and although the coral bleaching of 1997 in the JRNP was evaluated as very spread out in the area (Rey-Villiers et al. 2016), it could be the cause of high percentages of OM in 2001. Ten years later (2012), there was a significant decrease in OM on the reef crests and on the fore reef. This decrease could be a consequence of the replacement of large coral species by small, weedy coral species with quick growth and a short life cycle (Green et al. 2008). Rey-Villiers et al. (2016) found that in 2012 there *A. palmata* was replaced as the dominant species on the reef crests by *Porites astreoides* Lamarck, 1816 in comparison with the 2001 sampling. Hernández-Fernández (2021) reported that *Orbicella* spp. were replaced by *Agaricia agaricites* (Linnaeus, 1758) and *P. astreoides* on the fore reefs from 2001 to 2012. The change of species on coral reefs is a coral response to global stress (Bruno et al. 2019). This change of species causes a change in the reef structure and functioning, which largely determines community resilience according to Obura and Grimsdith (2009).

From 2001 to 2012, moderate El Niño events prevailed during the years 2002 and 2003, while weak El Niño events prevailed from 2004 to 2007, which could have influenced the decrease in the OM in 2012, as high temperatures did not prevail in this period. During the same period, La Niña events were weak in 2008 and 2009, strong in 2010-2011 and moderate in 2012 (Table 3, Fig. 9). During the years 2010 and 2011, severe heat-related stress affected the Caribbean area (Muñiz-Castillo et al. 2019). However, in the JRNP, moderate bleaching values were reported in 2010 and 2011, with affecting between 11% and 30% of the colonies (Alcolado 2011, 2012). The bleaching event of 2005 was the strongest in the Caribbean during the last 20 years, and mean regional temperature was the highest recorded in the last 150 years (Eakin et al. 2010). However, in the a JRNP bleaching-related damage was not significant in the short-term, because the impacted colonies recovered from the bleaching totally or partially (Hernández-Fernández et al. 2011).

The RM indicator is considered the most important evidence of the reef condition during the past year. A positive sign of reef recovery would be an average regional RM value of ≤2% (McField and Kramer 2008). In 2012, both habitats had the lowest value of RM, which could be related to date of sampling (April, before the warmest months of year).

A live coral cover of 15% to 20% would be a good parameter for assessing reef health and recovery (McField and Kramer 2008). On the fore reefs, coral cover values were above the mean reported for Cuba in these habitats (13.4%) between 2003 and 2009 (Alcolado et al. 2009), but below the mean reported for the Western Atlantic from 1999 to 2001 (26%) (Kramer 2003). Coral cover on the reef crests was below the mean reported for Cuba (17.6%) (Alcolado et al. 2009) and for the greater Caribbean region (25%) (Kramer 2003).

On the reef crests, coral cover was lower in 2012 than in 2001, which coincided with results from a previous study (Rey-Villiers et al. 2016). This decrease could be due to the effects of hurricanes, taking into account that this habitat is more severely impacted by these phenomena. From 2001 to 2012, three hurricanes and a tropical storm affected the study area directly or indirectly (Table 2). The worst damage of Hurricane Dennis, particularly to the branches of *A. palmata*, was on the reef crests, and other reef zones were less affected (Pina-Amargós et al. 2008a). Knowledge of the effects of hurricanes Paloma and Ike in the JRNP is limited to a small sector of seagrasses (Guimarais et al. 2013) and to a mangrove area in the western portion of the park, respectively (personal communication, Felipe Matos). Hurricane-related surge, waves and water movement have a significant effect on the structure and distribution of corals. Branching corals (e.g. *Acropora* spp.) are more vulnerable to wave damage than massive corals (e.g. *Porites* spp.). Accumulation and movement of coral debris generated by hurricanes and the increase in algae competing for space on the reef can make recovery difficult (Heron et al. 2008). Results regarding coral cover on the reef crests of the JRNP in 2017 could suggest that the ecosystem is recovering from the effects of the hurricanes and the tropical storm that hit the park in 2008.

An average regional recovery of five colonies m^{-2} could be a promising indicator of transitional reef recovery (McField and Kramer 2008). This value was recorded on the fore reefs, although it decreased from 2012 to 2017. There was an abrupt increase in recruit density in 2012 compared with 2001, as was also reported by Rey-Villiers et al. (2016).

Before 2017, there was a strong El Niño event (2015-2016) (Table 3, Fig. 9). Furthermore, the Caribbean region, and consequently the park area, was exposed to high temperatures from 2014 to 2017 (Muñiz-Castillo et al. 2019) (Fig. 3). There was a global bleaching event from 2014 to 2017 (Weiler et al. 2019), which affected the reefs of the park, specifically in 2015, with bleaching from moderate (11%-30%) to high (51%-75%) (Alcolado and Rey-Villiers 2016). This event could have caused the slight increase observed in the percentage of OM in 2017 in comparison with 2012 on the reef crests and on the fore reefs, taking into account that OM indicates the consequences of the distant past of the reef.

In 2017, the percentage of RM was higher than in 2001 and 2012, which could be related to the strong La Niña events that occurred before 2001 and 2012 (1999-2000 and 2010-2011, respectively) (Table 3, Fig. 9). La Niña events bring colder temperatures that limit the appearance of bleaching events, thus reducing the effect on corals and consequently the percentage of RM. A strong El Niño event occurred before 2017, during the years 2015 and 2016 (Table 3, Fig. 9). As reef crests are in shallow waters, they are more exposed to sunlight and consequently to higher SST, and this could be the cause of their higher percentage of RM in 2017. Although diseases are among the causes of coral RM (McField and Kramer 2008), some authors believe that they are the result of a complex interaction between corals, pathogens and the environment, but whether SST variations are related to these diseases is still unknown (Randall et al. 2014). In the JRNP, coral diseases are not directly studied, but some studies on reef crests and fore reefs reported no coral diseases (Hernández-Fernández et al. 2016b, Hernández-Fernández and Bustamante-López 2017, Hernández-Fernández et al. 2019a).

In 2017, coral cover in this habitat showed high values, even higher than those of 2012, but lower than those of 2001. The reef crests of the JRNP are formed by huge populations of *A. palmata*, which showed evidence of recovery in 2017 (Hernández-Fernández et al. 2019c). This fact could indicate that the reef crests of the JRNP need more than 10 years to fully recover from damage caused by global stressors such as hurricanes and SST rise, depending on their frequency. It has been documented that resilient coral reefs can recover from hurricane damage, as has happened in the Indo-Pacific and in Bonaire. The latter is the first example of a resilient reef in the Caribbean. It has recovered from severe climate-related mortality events in approximately seven years (Steneck et al. 2019). In addition, reefs located to the north of Jamaica have recently shown certain resilience four years after the impact of hurricanes and bleaching (Bruno et al. 2019).

CCA are an important component of the benthos in tropical seas (Steneck 1997) and favour the establishment of invertebrate larvae such as those of corals (Webster et al. 2011, Siboni et al. 2015). SST rise affects CCA and associated organisms, which consequently may affect recruitment on a coral reef (Webster et al. 2011, Johnson and Carpenter 2012). According to experimental evidence, CCA and related microbial communities do not tolerate SST of 32.0°C or variations of 2°C to 4°C above the SST annual maximum mean. After a seven-day period with temperatures of 32.0°C, they do not recover because of green algae bloom (Webster et al. 2011). It has been documented that a temperature rise of 28.0°C to 29.0°C has a negative effect on CCA, which results in an increase in fungi-related diseases (Williams et al. 2014). In August and September of 2015 and 2016, the warmest months of the year, mean temperature was 2°C to 3°C above the mean annual temperature, which could have affected the CCA, and consequently recruitment in 2017. These results were similar to those of a previous study (Hernández-Fernández and Bustamante-López 2019d). The effects of SST rise would have been more damaging on coral recruitment if local stress events had taken place in the area (Williams et al. 2014). The JRNP is a useful tool for protecting marine biodiversity and research on the resistance and recovery of coral communities and their responses to climate change. Some of the positive effects of MPA are a decrease in macroalgae and an increase in coral cover, which could be a cascade effect caused by protection of herbivore fishes (Birrell et al. 2008, Mumby et al. 2010). In the JRPN, Pina-Amargós et al. (2014) found effective protection from fishing and one of its consequences was an increase in abundance of ten fish species, including large herbivores (two species of parrotfish).

The significant differences between the zones of reserve showed the same result pattern for most indicators for the different years. However, these results confirm that although there is a protection gradient from the central zone to the east and west ends of the park, its influence on the status of coral and CCA communities is not clear (Hernández-Fernández et al. 2019b). This shows that reefs cannot be saved by local action alone, because their main degradation is due to anthropogenic climate change, which is the root cause of the global decline of reefs (Bruno et al. 2019).

The results of the present study show that the occurrence of hurricanes and SST behaviour could be the most probable causes of impacts on coral reefs in the JRNP in the study period. These negative effects on corals and CCA were more visible on the reef crests of the JRNP. Although the coral community may be totally different in its structure and functioning, it showed resistance and/or recovery capacity from the impacts suffered after 2001, suggesting some resilience between 2001 and 2012 (in a period of approximately 10 years), because it was mostly recovered after the disturbances that occurred in this period of time, which became evident until 2017, particularly for the coral cover.

The results of the present study could be used by decision makers, authorities and researchers as useful information for future management and monitoring strategies in the JRNP. The evidence that climate change is acting on coral communities has been documented by many authors cited in this study. The condition of an MPA does not, per se, reduce the effects of SST anomalies and hurricane frequency on coral communities, but it is an important tool for protection from other stressors, such as fishing, overexploitation of tourism and local stressors such as water pollution and wastewater discharges.

ACKNOWLEDGEMENTS

This study was financed by the project "Diversidad biológica y conectividad entre el archipiélago Jardines de la Reina y golfo de Ana María, Cuba", code P211LH005-031, of the National Programme of Conservation of Cuban Biodiversity (Ministry of Science, Technology and Environment of Cuba). We express our gratitude to the participants in the joint expedition CUBAGRRA II (August 2001), to the technicians and specialists of the Institute of Oceanology of Cuba, the Centre for Marine Research of the University of Havana, the Centre for the Research of Coastal Ecosystems, the Ocean for Youth vessel and the Jardines de la Reina Marlin branch. Our special thanks are due to Eduardo del Sol, Evelio A. Alemán, Roy Phillips, Claudia Bustamante, Noel López and Fabián Pina, and also to Vicente Osmel Rodríguez for his support with the English. IdeaWild org is thanked for equipment support.

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