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Biogeochemical responses of a highly polluted tropical coastal lagoon after the passage of a strong hurricane (Hurricane Irma)

Roberto González-De Zayas[a,b], Martín Merino-Ibarra[c,*], Julio A. Lestayo González[d], Yida Chaviano-Fernández[e], Miguel A. Alatorre Mendieta[f], Felipe Matos Pupo[g] and Fermín S. Castillo-Sandoval[c]

[a] Departamento de Ingeniería Hidráulica, Universidad de Ciego de Ávila, Carretera a Morón, Ciego de Ávila 65100, Cuba
[b] Centro de Estudios Geomáticos, Ambientales y Marinos (GEOMAR), Avenida Ejército Nacional 404, Polanco V Sección, Ciudad de México 11560, México
[c] Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México 04510, México
[d] Posgrado en Ciencias del Mar y Limnología, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México 04510, México
[e] Centro de Investigaciones de Ecosistemas Costeros, Cayo Coco, Morón, Ciego de Ávila 69400, Cuba
[f] Unidad Académica de Procesos Oceánicos y Costeros, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, Coyoacán, Ciudad de México 04510, México
[g] Centro Meteorológico Provincial, Ciego de Ávila, Avenida de los Deportes S/N, Ciego de Ávila 65100, Cuba
*Corresponding author. E-mail: mmerino56.unam@gmail.com

MM-I, 0000-0002-6690-3101

ABSTRACT

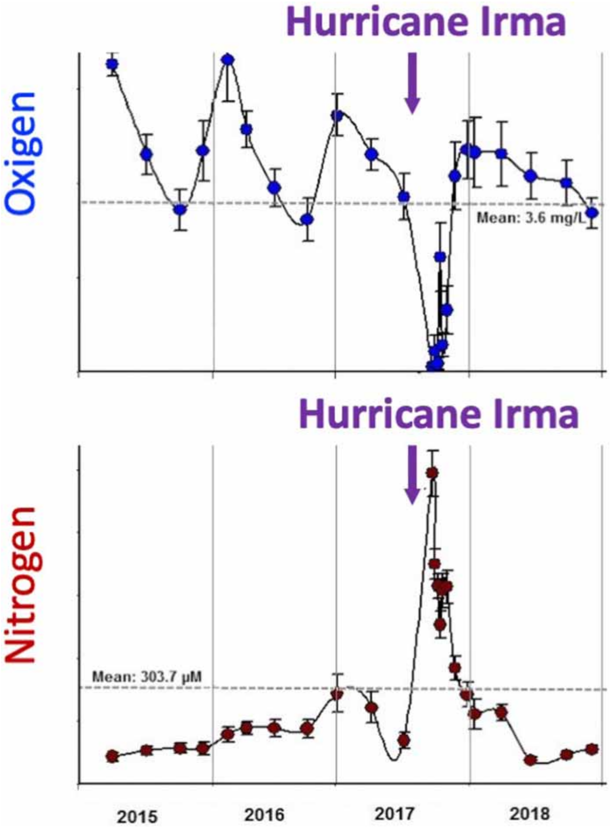
Laguna Larga (Cayo Coco, Cuba) is a eutrophic coastal lagoon due to tourism development. As part of long-term monitoring of Laguna Larga, we were able to follow the lagoon's water quality from 2015 to 2018 and could assess the impacts of Hurricane Irma (September 8–9, 2017) by intensifying our sampling frequency. Physicochemical parameters (salinity, pH, dissolved oxygen, dissolved inorganic nitrogen, dissolved reactive silicate and total nitrogen) exhibited significant variations associated with Hurricane Irma. Salinity decreased due to the extraordinary rainfall of the hurricane (339.8 mm/24 h, a new record for Cayo Coco). The water level in the lagoon rose 0.85 m. Strong hurricane winds and intense runoff drove organic matter and sediment resuspension. Anoxia and an increase of nutrients occurred throughout the lagoon. The main biogeochemical impact was that it boosted these eutrophic conditions of the lagoon, to levels that lasted for several months. A significant correlation among nutrients, salinity and dissolved oxygen was found. After 6 months, water quality in the lagoon had recovered to conditions similar to those before the hurricane. The case of Laguna Larga shows that those coastal systems under anthropic pressure can take longer to recover after extreme climatic events, and highlights the need for long-term monitoring of tropical coastal ecosystems.

Key words: biogeochemistry, Caribbean, eutrophic, resilience, management, nutrients

HIGHLIGHTS

- Long-term monitoring of eutrophic Laguna Larga continued even during the pass of Category 5 Hurricane Irma.
- The hurricane caused unprecedented impacts: extraordinary rain, water-level rise and a sharp salinity fall.
- Extended anoxia and extraordinary nutrient peaks boosted eutrophication.
- It took 6 months for the water quality of the lagoon to return to previous conditions.
- Anthropized lagoons may take longer to recover.

GRAPHICAL ABSTRACT



INTRODUCTION

Coastal lagoons are water bodies with restricted communication with the adjacent sea (Kjerfve 1994). They are ecologically diverse and provide habitats for many birds, fish and plants; the interactions among the species in estuaries and coastal lagoons produce valuable ecosystem services (Barnes 2001; Harris 2008). At the same time, there are multiple anthropogenic stressors acting on many coastal lagoons, including sewage and organic wastes, derived eutrophication, sea-level rise, and habitat disturbance and loss (Kennish & Paerl 2010; Raji *et al.* 2013; González-De Zayas *et al.* 2013, 2018; Chacón Abarca *et al.* 2021). The effects of these stressors on coastal lagoons and estuaries can be more destructive when there is a combination of two or more due to the cumulative impacts. In particular, these stresses can coincide with the impacts of hurricanes and extreme climatic events, which are expected to increase their frequency, intensity and stochasticity as a result of climate change (Bender *et al.* 2010; Knutson *et al.* 2015; Hampel *et al.* 2019; Neilson *et al.* 2020).

However, extreme climatic events can exert multiple impacts on coastal lagoons, and their response to these disturbances is likely complex. In any case, these responses likely depend on the vulnerability and the resilience of the lagoon (Barnes 2001; Harris 2008; Kennish & Paerl 2010; Patrick *et al.* 2020). Some of the most direct impacts of extreme climatic events, and in particular storms and hurricanes, on coastal lagoons are derived from the strong winds (Walker *et al.* 2021a). These include changes in wave height and storm surges (Raji *et al.* 2013), alteration of the circulation patterns and the associated sediment resuspension (Forsberg *et al.* 2018). Another important direct impact comes from extraordinary rainfall and the derived flooding (Herbeck *et al.* 2011; Hampel *et al.* 2019; Patrick *et al.* 2020; Phlips *et al.* 2020), which can be enhanced by the storm's surge. Flooding and extraordinary runoff can: (1) directly alter salinity (Kowalski *et al.* 2018; Walker *et al.* 2021a), (2) increase or decrease nutrients concentration (Barik *et al.* 2017; Hampel *et al.* 2019; Steichen *et al.* 2020; Clementson *et al.* 2021; Walker *et al.* 2021b), (3) significantly increase the suspended organic matter (Herbeck *et al.* 2011), (4) cause drastic declines in the oxygen concentration (Hampel *et al.* 2019) and (5) alter the abundance and composition of benthic (Bhadury *et al.* 2018) and plant (Hanley *et al.* 2020) communities.

The wind itself can also cause significant damage to vegetation, in particular to mangroves, which are frequently an important fringing component of coastal lagoons (Walcker *et al.* 2019). Additionally, vegetation debris derived from its destruction can become an important additional input of organic matter and nutrients to the water body (Bhadury *et al.* 2018; Hampel *et al.* 2019). Several of these impacts (strong currents an erosion, sediment resuspension, nutrient increase and anoxia) can affect benthic communities and generate long-term alterations on these communities (Bhadury *et al.* 2018) and the biogeochemical processes associated with them (Middelburg & Levin 2009). In spite of this, although the impacts of hurricanes on land ecosystems and human populations are very well documented, there is a scarcity of reports on the impacts on coastal lagoons, and particularly, on their recovery after hurricane alterations.

The Caribbean Region has been particularly affected by the increase in the frequency and intensity of tropical storms and hurricanes during the last two decades (Chen *et al.* 2009; Quiñones-Rivera *et al.* 2010; Chen *et al.* 2017; Kowalski *et al.* 2018; Rivera-Monroy *et al.* 2020). How coastal lagoons have been affected and are dealing with the impacts derived from this increase has not been thoroughly studied and evaluated (Paperno *et al.* 2006; Galván *et al.* 2012; Feller *et al.* 2015; Chen *et al.* 2017; Kowalski *et al.* 2018; Hanley *et al.* 2020). At the same time, the vulnerability of coastal lagoons in the Caribbean Region is likely increased due to the rising trend of sewage disposal and nutrient enrichment to the coastal zone derived from tourism development in the region (Paperno *et al.* 2006; Perigó *et al.* 2006; González-De Zayas *et al.* 2013, 2018; Feller *et al.* 2015; Chen *et al.* 2017; Walker *et al.* 2021b).

In Cuba, the studies on coastal lagoons are relatively scarce and are focused mainly on their ecological characterization (González-Sansón & Aguilar 1984; Lalana 1986; Guimarais-Bermejo & González-De Zayas 2011) or on direct human impacts (i.e., tourism development, industrial and domestic sewage disposal) (Pérez Santos *et al.* 2003; Perigó *et al.* 2006; Perigó *et al.* 2009; González-De Zayas *et al.* 2013). However, the combined impact of natural (hurricanes) and anthropogenic stressors (sewage disposal, dredging) has barely been reported, except for the effects of Hurricane Kate (1985) over water quality of a polluted brackish lagoon (Gómez-Carro *et al.* 1988), and the effects of Hurricane Dennis on the macrophytobenthos of the Bay of Cienfuegos (Moreira *et al.* 2009).

One of the few coastal lagoons in Cuba where long-term monitoring has taken place is Laguna Larga, located in Cayo Coco. Water quality has been assessed since 2007 in this shallow (<1.0 m in mean depth) and chocked coastal lagoon, around which important tourism infrastructure has been constructed (González-De Zayas 2012, 2013). The anthropisation of this lagoon derives mainly from tourism activity. Four large hotels with nearly 3,000 rooms are built around or on the lagoon itself, and over 150,000 visitors/year have made Laguna Larga a polluted tropical coastal lagoon where nutrients and eutrophication clearly increased in just a few years (González-De Zayas *et al.* 2018).

Cayo Coco and Laguna Larga are along the main track of hurricanes in the Caribbean Region (Gómez-Carro *et al.* 1988; Moreira *et al.* 2009). However, only tropical storms passed through the area from 1999 to 2015, until in October of this year Hurricane Joaquín passed near Cayo Coco area, and on September 8–9, 2017, Hurricane Irma struck directly over Laguna Larga (Table 1). Hurricane Irma was the strongest and most intense storm in the Atlantic since 2005 (Cangialosi *et al.* 2018) and the most powerful hurricane that has struck the northern Caribbean over the last 100 years (Walcker *et al.* 2019). It reached Category 5 and caused catastrophic damage in the northeastern Caribbean and the Florida Keys. It developed on August 30, 2017, near the West coast of Africa and became a hurricane according to the Saffir–Simpson scale within 1 day. Irma became a major Category 3 storm on September 5, 2017; then reached its peak as a Category 5 hurricane with winds of 185 mph (295 km/h) (Cangialosi *et al.* 2018). Irma made landfall in Cayo Coco as a Category 5 and winds over 100 km/h (between September 8th and 9th, Figure 1), with wind gusts of up to 194 km/h (Irma was the first hurricane of Category 5 to landfall in Cayo Coco since 1851). The storm brought very heavy rains to the area and caused severe damage to the forests and mangroves of the island. It also devastated tourist areas not only of Cayo Coco but also of Cayo Guillermo and Cayo Santa Maria. Greater damages occurred at Morón city and other towns near of north coast of Ciego de Ávila Province.

In this paper, we rely on physicochemical and biogeochemical data obtained in Laguna Larga used as part of a long-term monitoring program, to assess: (1) the evolution of the water quality of the lagoon from 2015 to 2018, (2) the influence of Hurricane Irma on the lagoon's water quality and (3) the recovery of the lagoon after the impact of Hurricane Irma. Because of resource limitation, the monitoring was done quarterly, but as the hurricane passed, we managed to increase the sampling frequency to weekly, so that a detailed follow-up of the impacts of the hurricane in Laguna Larga could be obtained.

Table 1 | Tropical storms (including hurricanes) that affected Cayo Coco between 1985 and 2017

Name	Date of storm formation	Date of influence over Cayo Coco	Category at date of influence
Kate	November 15, 1985	November 19, 1985	H2
Lili	October 14, 1996	October 19, 1996	H1
Georges	September 15, 1998	September 24, 1998	H1
Michelle	October 29, 2001	November 5, 2001	TS
Chris	July 31, 2006	August 5, 2006	TD
Ernesto	August 24, 2006	August 29, 2006	TS
Noel	October 23, 2007	October 31, 2007	TS
Ike	September 1, 2008	September 8, 2008	TS
Paula	October 10, 2010	October 16, 2010	TD
Isaac	August 20, 2012	August 26, 2012	TS
Joaquin	September 27, 2015	October 2, 2015	H2
Irma	August 29, 2017	September 9, 2017	H5

TD: tropical depression; TS: tropical storm; H: hurricane, the number indicates the category.

MATERIALS AND METHODS

Meteorological data and hurricane information

Daily reports from station 339 of the Cuban Network of Meteorological Stations, located in Cayo Coco, were used to study the temporal evolution of rainfall. The period 1990–2016 was used as a historical climatic reference. Data from Hurricane Irma reports were also revised. Irma was a long-lived Cape Verde hurricane that reached Category 5 on the Saffir–Simpson Hurricane Wind Scale. Irma landed near Cayo Romano, Cuba, with estimated maximum winds of 268 km/h. The lowest pressure recorded in Cuba during Hurricane Irma's pass was 933.1 hPa at Cayo Coco, at 0520 Coordinated Universal Time (UTC) on September 9, in the eye of the hurricane. The western eyewall was also sampled at that station. Sustained winds of 154 km/h and a gust of 194 km/h were recorded at 0500 UTC that day. The highest wind speed recorded in Cuba was in an inland area of Cayo Coco, where sustained winds of 200 km/h and a gust of 256 km/h were measured at 0720 UTC on September 9. The Institute of Meteorology of Cuba reported that Irma produced significant flooding along the northern coast of Cuba due to storm surge and large waves. In Ciego de Ávila Province, the sea rose by 3–3.5 m and penetrated more than 800 m inland. Wave heights in Cayo Coco were estimated between 5 and 6 m. Figure 2 shows the spectral significant wave height (Hm0 on September 9, which reached >10 m) in the Bahamas Channel, which ranged between 5.5 and 6.5 m in Cayo Coco and the Cuban coast.

Study area

Laguna Larga is a small (67,059 m^2) tropical coastal lagoon located (22.538°N, 78.365°W) in Cayo Coco, an island of the Sabana-Camaguey Archipelago in the northern coast of central Cuba (Figure 3). Previous publications have documented the anthropic impacts on the lagoon and its conditions between 2007 and 2009 (González-De Zayas & Merino-Ibarra 2010; González-De Zayas *et al.* 2013, 2018). The lagoon has been extensively altered by the construction of four large hotels along its basin and on the lagoon itself (González-De Zayas 2012). The lagoon is elongated, and only narrow channels fringed by mangroves connect the inner (western), central and outer (eastern) sections of the lagoon (González-De Zayas *et al.* 2018). The lagoon is very shallow in the central (0.3–0.5 m, stations 6–8, Figure 3) and outer (0.5–0.8 m, stations 1–5 Figure 3) sections. Depth reaches >1.0 m only in the inner section (1.0–1.2 m, stations 9–12, Figure 3), because it was dredged. Tides have very small amplitude in the region, and the lagoon has a very high residence time, that increases from the outer to the inner section (González-De Zayas & Merino-Ibarra 2010). Laguna Larga is particularly choked because its natural communication with the sea is restricted only to a single narrow channel (8–15 m wide) located in one of its extremes (González-De Zayas *et al.* 2013). Because of its choked nature and the atrophic impacts, the lagoon is eutrophic and exports nitrogen and phosphorus to the sea (González-De Zayas *et al.* 2013, 2018). Primary producers are dominated

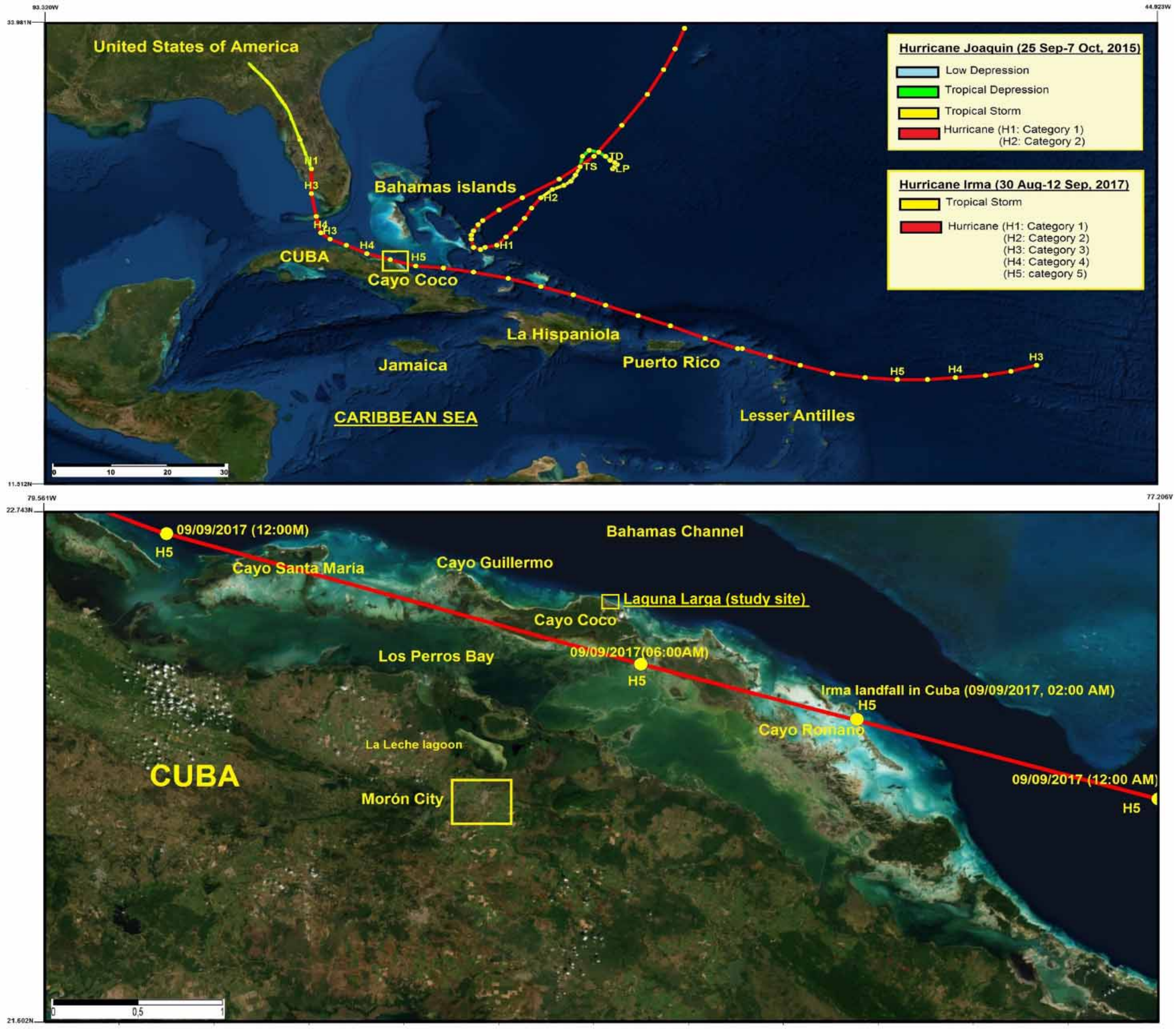


Figure 1 | Tracks of Hurricane Joaquin and Hurricane Irma in the Caribbean in the superior image, and below the trajectory of Irma over Cayo Coco (Cuba).

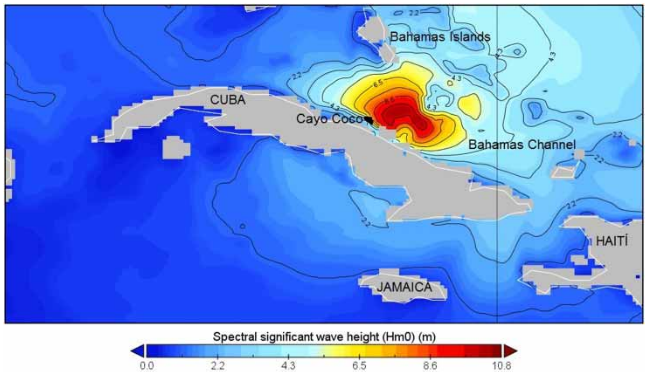


Figure 2 | Increase of spectral significant wave height (Hm0) near Cayo Coco during Hurricane Irma (September 8–9, 2017) (Data from Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu/).

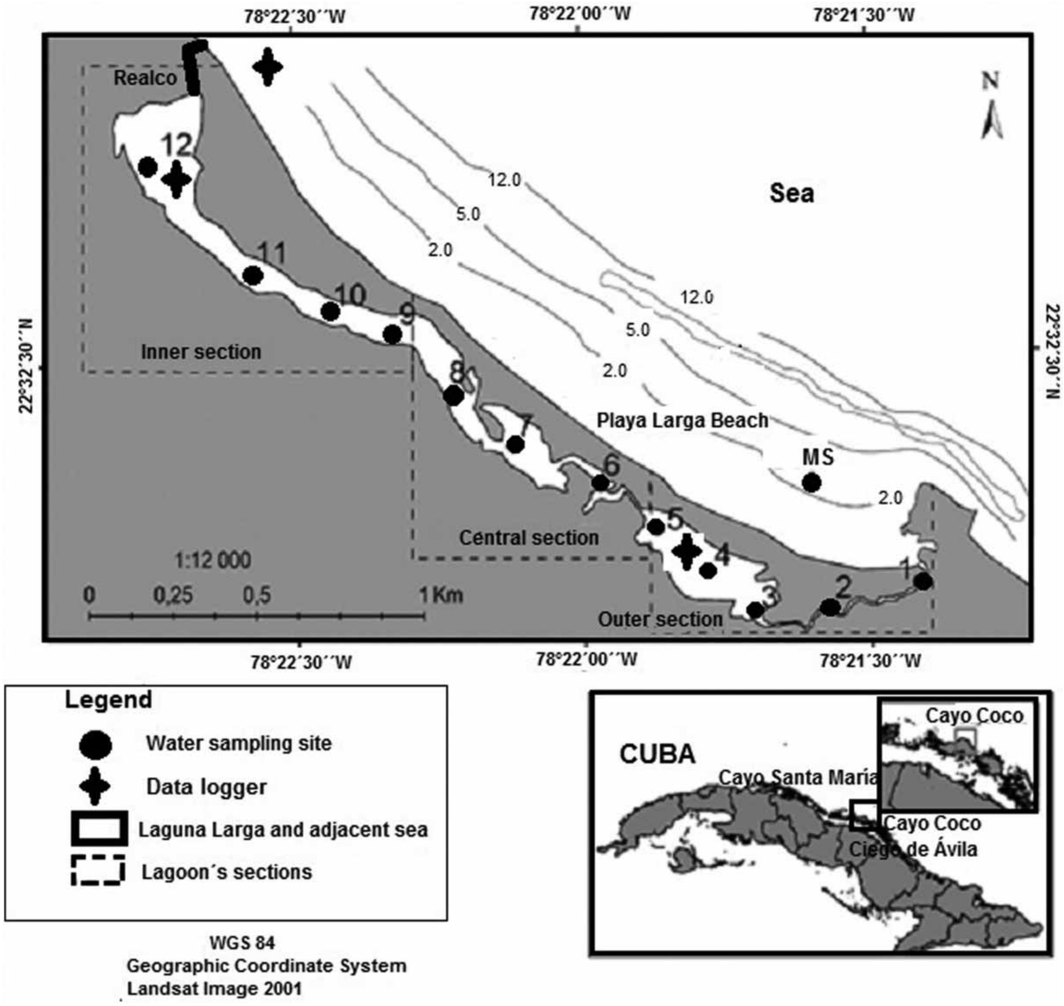


Figure 3 | Map of Laguna Larga with sampling sites, its sections, location of the water-level loggers and other details.

by phytoplankton in the central and interior sections, but marine phanerogams (*Ruppia maritima*, *Halodule wrightii* and *Thalassia testudinum*) can still be found in the outer section (Guimarais-Bermejo & González-De Zayas 2011). Similarly, mollusk assemblages also show major differences between the lagoon sections (Olivera 2014).

Human impact on the system is due to international tourism (more than 150,000 visitors per year), the main economic activity in the area, because hotels and other facilities discharge sewage directly or indirectly to the lagoon. This anthropic impact has increased significantly: in 1993 there were only 400 rooms for tourism, increasing to more than 3,000 rooms after 2001. The lobby of one of the hotels (Tryp Hotel: more than 500 rooms) was built on top of the lagoon (at station 9, Figure 3), further restricting the water flow at this point, where the hotel's sewage is also discharged (cf. González-De Zayas 2012 for more details).

Sampling and sample analysis

Sampling was carried out quarterly between 2015 and 2018 (Table 2) over a site network distributed throughout the lagoon (12 sites), and a reference site (MS) in the adjacent coastal sea (Figure 3), following the same monitoring strategy used between 2007 and 2009 by González-De Zayas *et al.* (2013, 2018), to facilitate comparison. Nevertheless, to obtain a better temporal resolution of the evolution of impacts of the hurricane on the lagoon, the sampling frequency was increased from quarterly to weekly right after the hurricane passed and was gradually decreased as the system recovered.

Table 2 | Sampling details (2015–2018) in Laguna Larga

Sampling ID	Sampling frequency	Date	Remarks
1	~ Quarterly	April 2, 2015	Before
2	~ Quarterly	July 7, 2015	Before
3	~ Quarterly	October 8, 2015	Before (hurricane Joaquin passed at north of study site)
4	~ Quarterly	December 11, 2015	Before
5	~ Quarterly	February 18, 2016	Before
6	~ Quarterly	April 11, 2016	Before
7	~ Quarterly	June 28, 2016	Before
8	~ Quarterly	September 28, 2016	Before
9	~ Quarterly	December 21, 2016	Before
10	~ Quarterly	March 28, 2017	Before
11	~ Quarterly	June 26, 2017	Before
Hurricane Irma passed over the study site		September 8–9, 2017	
12	~ Quarterly	September 14, 2017	After
13	~ Weekly	September 21, 2017	After
14	~ Weekly	September 29, 2017	After
15	~ Weekly	October 6, 2017	After
16	~ Weekly	October 12, 2017	After
17	~ Fortnightly	October 26, 2017	After
18	~ Fortnightly	November 16, 2017	After
19	~ Monthly	December 20, 2017	After
20	~ Monthly	January 11, 2018	After
21	~ Quarterly	March 27, 2018	After
22	~ Quarterly	June 16, 2018	After
23	~ Quarterly	September 24, 2018	After
24	~ Quarterly	December 4, 2018	After

Temperature and salinity were determined *in situ* using a WTW digital thermo-salinometer. Dissolved oxygen (DO) was determined in triplicate by the Winkler method (Wright 1983). Nutrient samples (dissolved inorganic nitrogen ($DIN = NH_4^+ + NO_2^- + NO_3^-$) and soluble reactive phosphorus (SRP)) were immediately filtered through Millipore filters of 0.22 μm and fixed with chloroform. Filtered samples were frozen until analysis, together with unfiltered samples for total nitrogen (TN) and phosphorus (TP). Dissolved nutrients were analyzed with a Skalar San Plus segmented-flow autoanalyzer using the standard methods adapted by Grasshoff *et al.* (1983) and the circuits suggested by Kirkwood (1994) at the Marine Biogeochemistry Laboratory at ICML, UNAM. TN and TP were analyzed as nitrate and SRP after high temperature (120 °C) oxidation with persulfate for 30 min, following Valderrama (1981). Organic nitrogen and organic phosphorus were calculated by subtraction (see González-De Zayas *et al.* (2013) for details).

Water-level records

HOBO data loggers placed inside Laguna Larga and in the adjacent oceanic waters (from 2012 to 2016) north of Laguna Larga (Figure 2) were used to record water level and temperature every 2 min. Monthly data were processed with the software HOBOware Pro, version 3.7.13. These water-level measurements were used to calculate the volume of water that overflooded the lagoon after Hurricane Irma passed, multiplying the water-level variation (mean: 0.85 m) measured by the two different HOBO data loggers in the lagoon by the area of the lagoon.

Statistical analysis

To determine data normality, a Shapiro-Wilk's *W* test was performed for all parameters surveyed. Because most data exhibited normal distributions, we used an ANOVA test and a post-hoc Tukey test to find significant differences among surveys, with sampling date as an independent effect in the model and each measured physicochemical variable as a dependent variable. The Pearson correlation was used to determine a significant correlation among measured physicochemical parameters. Using the principal components analysis (PCA) allowed the total variability of water quality (using measured parameters) to be analyzed, and also the association of these parameters with their temporal distribution. The first (PC1) and second (PC2) principal components from the analysis were plotted to infer temporal differences in water quality. PCA also has the advantage of allowing the identification of general tendencies and relationships among water quality variables through the examination of factor loadings of each variable on PC1 and PC2. The STATISTICA Program (Version 10.1) was used for all the analyses.

RESULTS

Rainfall and storm surge

A new historic record of 339.8 mm of rainfall in a 24-h period was recorded in Cayo Coco during the passing of Hurricane Irma. At the same time, a sharp rise in the water level was also registered (Figure 4) by two data loggers placed in the lagoon, which reached an average maximum of 0.85 m relative to the previous mean level. The sea level also rose over the dunes that separate Playa Larga from the sea, contributing to the flooding of the lagoon. These conditions remained for around 40 h; then water level went back to normal in both sections of the lagoon.

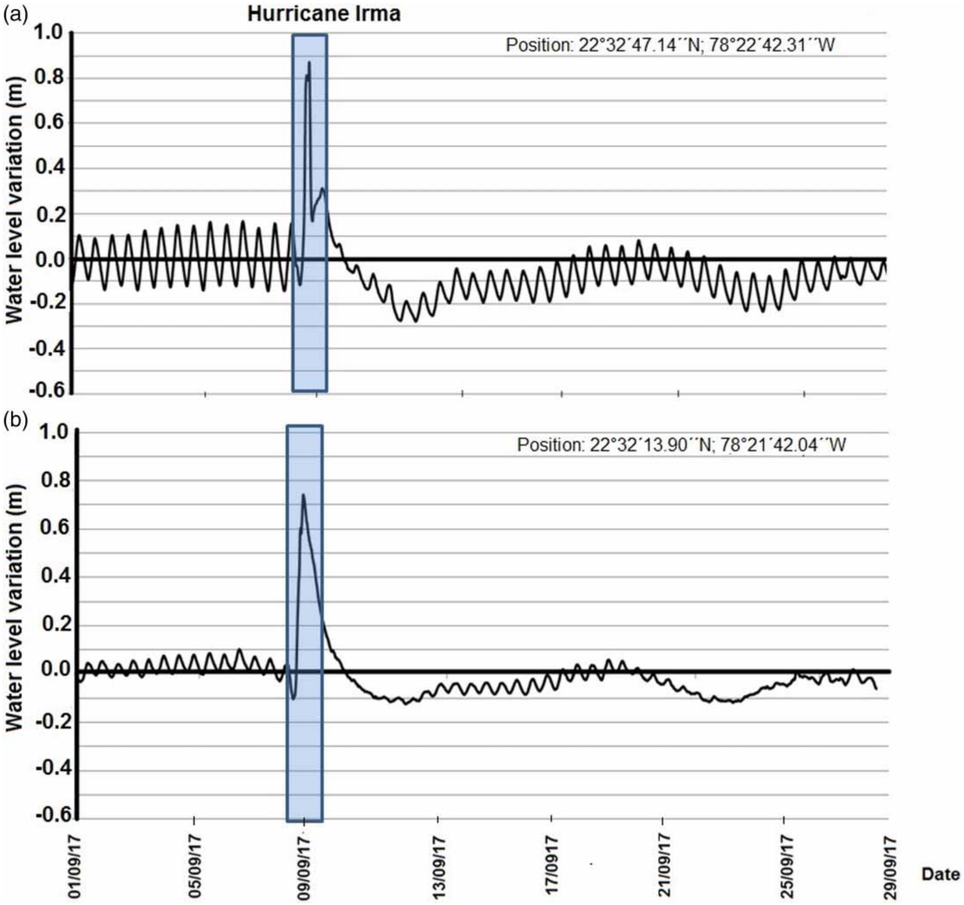


Figure 4 | Water-level variation (m) in (a) the western section and (b) the eastern section of Laguna Larga, from September 1 to 29, 2017. The blue rectangles outline the water-level variation from September 8 to 9, during the passage of Hurricane Irma.

Variation of physicochemical and biogeochemical parameters

Before the passing of Hurricane Irma, the salinity within Laguna Larga followed a seasonal pattern with relatively small oscillations (Figure 5(a)). Overall mean salinity was 31.2 ± 5.6, with the highest salinities in October of 2015 (36.9 ± 0.6) and June of 2016 (36.4 ± 0.6) (Figure 5(a)). However, after the hurricane, salinity decreased notoriously, reaching historical minimums of salinity in October 2017 (21.6 ± 5.4) and January 2018 (23.4 ± 3.2). Statistically, the differences of salinity among samplings were significant ($F = 20.65$, $p < 0.05$). The post-hoc Tukey analysis showed three groups of values. The dry months' samplings, with salinities over 32.0, were grouped together in one of them, the rainy winter samplings were pooled together in a second group similar to the overall salinity mean (Figure 5(a)) and a third group in which most of the samplings after Hurricane Irma, with salinities below 30.0, were placed. Salinity also showed significant correlations with DO, SRP, soluble reactive silicate (SRSi), dissolved inorganic nitrogen (DIN) and TN (Table 3).

Water temperature also showed typical seasonal oscillations (Figure 5(b)), but did not change as notoriously as the hurricane passed the study zone, although higher mean temperatures (32.7 ± 2.3°C) were recorded during the first samplings after Hurricane Irma (September 14 and 21, 2017). The temperature averaged 28.3 ± 2.5°C during 2015–2018 and ranged from 22.8 to 35.2°C. Temperature differences among ($F = 39.20$, $p < 0.05$) samplings were also significant. Water temperature showed an inverse significant relationship with DO ($r = -0.63$) and pH ($r = -0.44$) (Table 3) during the sampling period.

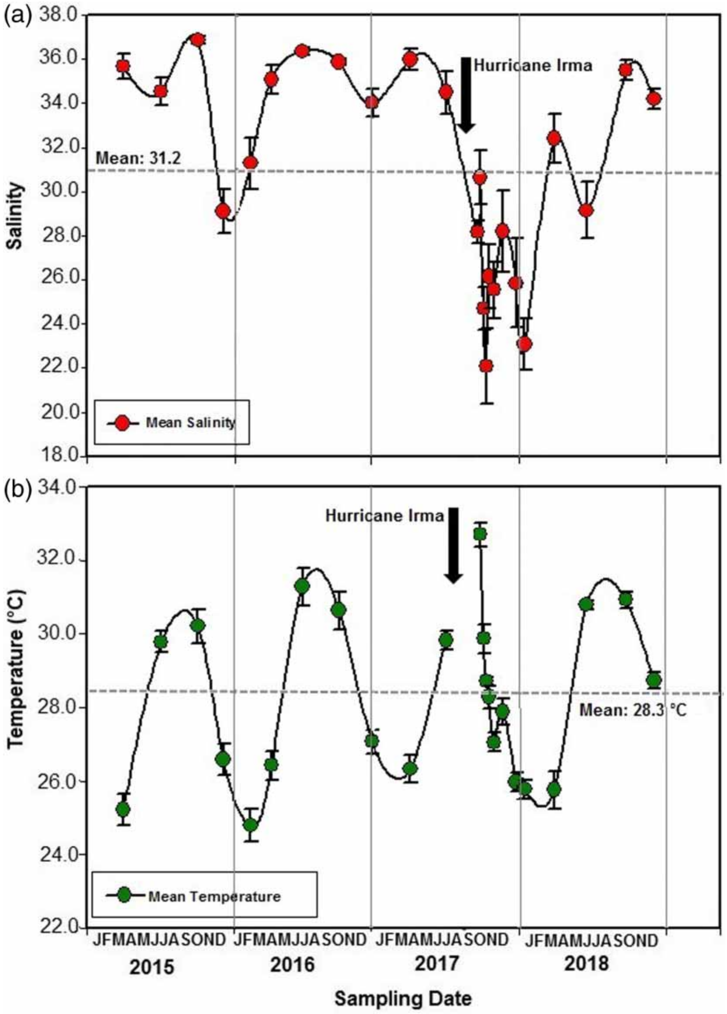


Figure 5 | Plots of (a) salinity and (b) temperature inside Laguna Larga (2015–2018). Circles represent mean concentration and bars represent standard error. The black dotted horizontal line represents the mean, and the vertical black arrow represents the date Hurricane Irma passed over the study zone.

Table 3 | Pearson's correlation matrix of physicochemical parameters measured in Laguna Larga during the sampling period 2015–2018

	Salinity	DO	pH	Temperature	SRP	SRSi	DIN	TP	TN
Salinity	1.000								
DO	0.444*	1.000							
pH	0.386	0.665*	1.000						
Temperature	0.144	−0.628*	−0.448*	1.000					
SRP	0.474*	0.188	−0.057	0.101	1.000				
SRSi	−0.567*	−0.794*	−0.348	0.320	−0.247	1.000			
DIN	−0.676*	−0.824*	−0.614*	0.302	−0.167	0.805*	1.000		
TP	−0.058	−0.006	−0.121	−0.210	0.295	−0.014	0.215	1.000	
TN	−0.603*	−0.843*	−0.505*	0.307	−0.187	0.909*	0.955*	0.121	1.000

*Significant correlation.

The pH of the lagoon remained between 7.60 and 8.34, with a mean of 7.92 ± 0.19. ANOVA and post-hoc Tukey tests showed that pH was more stable than other parameters for all samplings, with a significant drop immediately after the hurricane ($F = 12.08$. $p < 0.05$). However, pH quickly stabilized and recovered (October 26, 2017) to its pre-hurricane values, recorded in June 2017. pH had a significant positive correlation with DO and a negative correlation with water temperature, DIN and TN (Table 3).

Like salinity and temperature, DO also showed significant differences among samplings ($F = 15.11$, $p < 0.06$) and a strong correlation with salinity, temperature, SRSi, DIN and TN (Table 3). Before Hurricane Irma, DO within the lagoon ranged between 0.7 and 10.3 mg/L (mean of 4.7 ± 2.0 mg/L) with some hypoxia episodes (October 2015; February 2015; September 2016 and June 2017), particularly at site 9, where the principal sewage discharges are located and where the lagoon geomorphology has been more impacted by hotel construction. During the first sampling after the hurricane (September 14), DO dropped sharply to only 0.1 mg/L, and generalized anoxia was found throughout the lagoon (Figure 6(a)) accompanied by high fish mortality. These anoxic conditions prevailed until October 6 (2.4 mg/L), but returned to the previous levels during the following sampling. The lagoon recovered its normal mean DO levels 2 months after the hurricane (November 2017), except at sites 8 and 9, where it took DO levels 3 months to recover.

Following a pattern opposite to that of DO, nutrients peaked after Hurricane Irma passed over Laguna Larga. Mean SRSi concentrations peaked up to 130.2 μM after Hurricane Irma (Figure 6(b)), and returned to 7.5 μM by December 2018, similar to the basal levels it had in 2015. This nutrient had marked correlations with salinity, OD, DIN and TN. There were significant differences of SRSi among samplings ($F = 13.74$, $p < 0.05$), which were pooled into three groups of mean concentrations: one group below 40.0 μM, another around the mean concentration (51.4 μM), and a third group (samplings immediately after the hurricane) with concentrations over 80.0 μM, that was statistically different from other two groups according to the post-hoc Tukey analysis.

Mean concentrations of DIN ranged between 3.2 and 357.0 μM (88.7 ± 187.3 μM) and the highest concentrations (more than 70 times the previous sampling, $F = 32–5$, $p < 0.05$) occurred immediately after the hurricane. After December 2017 (3 months after the hurricane), mean DIN levels were similar (without significant differences) to DIN levels before the hurricane. NH_4^+ concentrations were around 70% of DIN before the hurricane, but after it, the percentage increased to 99% and prevailed for 3 months. DIN concentrations represented a low percentage (2–23%) of TN before Hurricane Irma, but after the hurricane, it increased to 51% and it was not until March 2018 that it recovered its previous proportion.

TN exhibited a marked correlation with DIN, SRSi, salinity and DO (Table 3), and a temporal pattern similar to that of SRSi, reaching significantly higher ($F = 44.11$, $p < 0.05$) mean TN concentrations after the hurricane (Figure 6(c)). On September 14, TN rose up to 953.1 ± 251.6 μM, much higher than pre-hurricane concentrations (from 85.9 to 287.4 μM) and remained high for 3 months (until November 2017). The post-hoc Tukey analysis showed that, after December 2017, the mean TN was similar (without significant differences) to those of the samplings prior to the hurricane.

Phosphorus was relatively low in Laguna Larga during the entire period and perhaps the limiting nutrient. The mean SRP concentration for the entire study period was only 0.2 ± 0.2 μM and remained relatively stable during

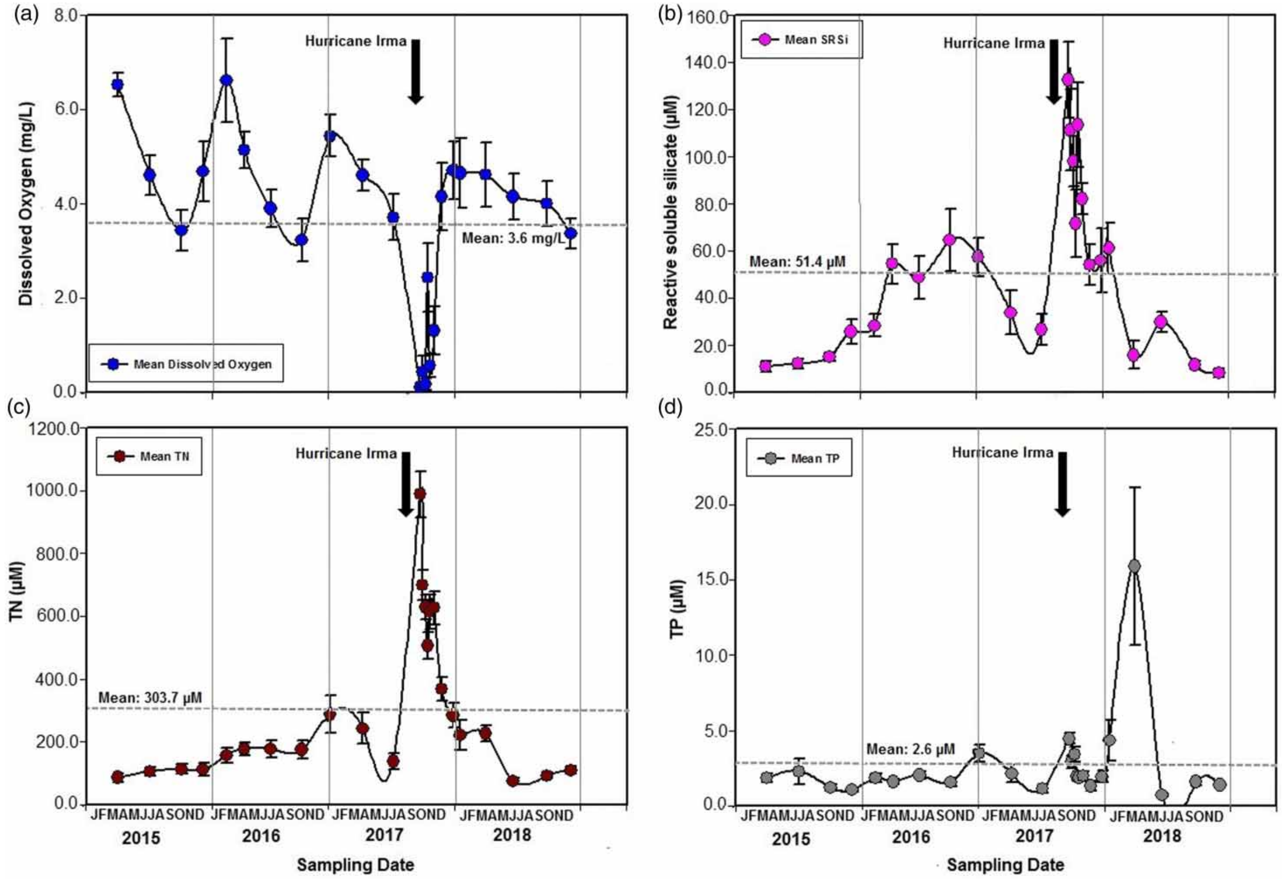


Figure 6 | Plots of (a) dissolved oxygen, (b) soluble reactive silicate (SRSi), (c) total nitrogen (TN) and (d) total phosphorus (TP) inside Laguna Larga (2015–2018). Circles represent mean concentration and bars represent standard error. The black dotted horizontal line represents the mean and the vertical black arrow represents the date of Irma over the study zone.

the hurricane passage. SRP only represented around 10% of TP. Mean TP concentrations were also relatively stable around a mean of 2.6 μM, but it did show an increase as the hurricane passed. A maximum of up to 15.9 μM in TP was observed later, in March 2018 ($F = 7.71$, $p < 0.01$, Figure 6(d)). TP did not correlate significantly with any other parameter.

ANOVA and subsequent post-hoc Tukey showed overall significant differences between the samplings before and after Hurricane Irma. The samplings after the pass of the hurricane were similar among them after January 2018. The PCA (Figure 7) also showed that the water quality of Laguna Larga was not the same before and after Hurricane Irma. The lagoon returned to the physicochemical conditions previous to Hurricane Irma after 6 months (March 2018, Figure 7, sampling 21), with a transition period from November 2017 to January 2018.

Comparison of the sampling sites through PCA (using all measured parameters) before and after the hurricane is shown in Figure 8. The main component, PC1, outlines the differences in water quality among the samplings performed before and after the hurricane (samplings of 2018) and how the site's distribution went back to a status similar but not equal to the one they had before the hurricane. This trend is associated with the concentrations of salinity, SRSi and TN. The second component, PC2, is related to the variation of the climatic season (temperature), as well as the influences of DO, DIN and SRP (Figure 8).

DISCUSSION

The results presented here document the strong impacts of Category 5 Hurricane Irma on the tropical lagoon of Laguna Larga, which included drastic changes in the water level, salinity, DO and nutrients. As described in the 'Results'

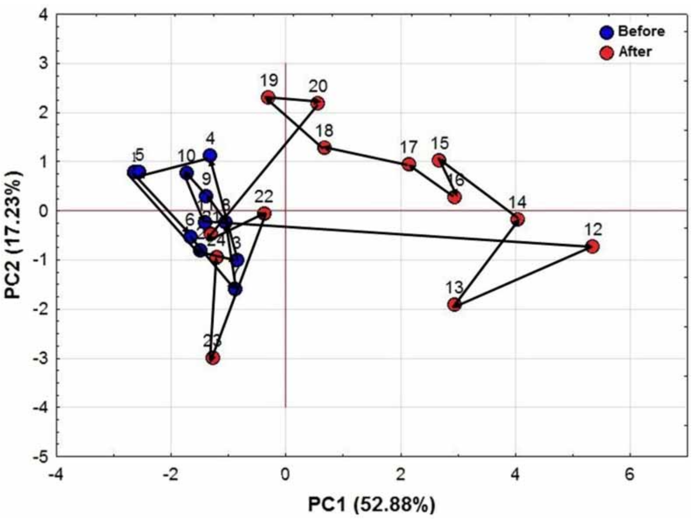


Figure 7 | PCA of the 2015–2018 sampling period and the relationship between PC1 and PC2 factors. Blue and red circles represent samplings before and after Hurricane Irma, respectively. Numbers are samplings sequential ID, as in Table 2.

section, the water quality in Laguna Larga deteriorated dramatically as a result of the hurricane passage and did not recover to a level similar to the previous conditions until 6 months later. The impact of Hurricane Irma in Laguna Larga is unprecedented for the area. Storms that hit Cayo Coco in the last 20 years left no comparable impacts. Precipitation from Hurricane George was 20.9 mm, and no related impacts were documented. Hurricane Joaquin (October 1–2, 2015) missed Cayo Coco and moved approximately 300 km to the northeast across central and southeastern Bahamas. Laguna Larga was sampled 6 days after Joaquin, and it showed only a small increase in salinity (from 34.5 ± 2.2 in the previous sampling to 36.9 ± 0.6).

In contrast, the water balance of this choked lagoon (González-De Zayas *et al.* 2013) with important anthropogenic discharges (González-De Zayas *et al.* 2018) was altered notoriously by the extraordinary rainfall brought by Hurricane Irma.

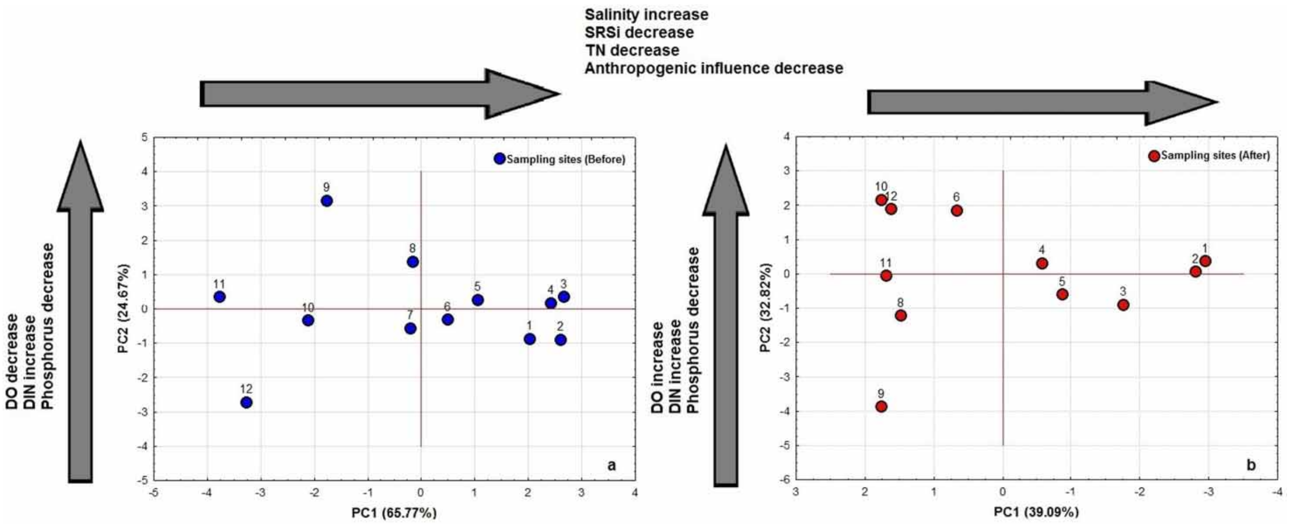


Figure 8 | PCA of sampling sites inside Laguna Larga: (a) before Hurricane Irma and (b) after the hurricane (samplings of 2018) and the relationship between PC1 and PC2. Arrows represent the influence of physicochemical parameters in both principal factors (PC1 and PC2). Blue circles represent the sampling sites before and red circles represent the sampling sites after Hurricane Irma. The numbers identify the sites as in Figure 2.

Because of the concurrent storm surge in the adjacent ocean, rainfall caused a drastic salinity fall as it remained flooding the lagoon and its surrounding drainage areas (González-De Zayas & Merino-Ibarra 2010). Similar salinity decreases associated with hurricanes and storms have also been reported for other shallow coastal lagoons (Gómez-Carro *et al.* 1988; Chen *et al.* 2017; Kowalski *et al.* 2018) and bays (Moreira *et al.* 2009) due to the magnitude of rainfall. High freshwater discharges after a strong hurricane have also been documented over Chilika Lagoon, Pamlico Sound and Neuse River Estuary (Barik *et al.* 2017; Paerl *et al.* 2018). In the case of Laguna Larga, the duration of flooding and intensity of the salinity decrease were likely enhanced by the lagoon's particularly choked nature due to the restriction of its communication with the sea by its single inlet and narrow channel (González-De Zayas *et al.* 2013).

The combined effects of flooding and the strong hurricane winds likely caused sediment resuspension in Laguna Larga due to the shallowness of the lagoon, particularly in its central and outer sections (González-De Zayas *et al.* 2013), and the 5 and 6 m wave heights caused by the hurricane passage through Cayo Coco. This is also consistent with indication by the drastic anoxia and the concurrent increases in nutrients observed after the passage of Hurricane Irma. The importance of oxygen as perhaps the most useful proxy for water quality in aquatic ecosystems can hardly be overstated. Mee (1988) used it to define critical eutrophication, and it is always considered when assessing water quality. Oxygen is critical for the survival of aerobic organisms, including all the macrofauna. As oxygen is depleted, biogeochemical processes, both in the water column and the sediments, change drastically as a function of the redox conditions (Middelburg & Levin 2009). The decrease in oxygen concentration in Laguna Larga (Figure 6(a)) outlines very well the magnitude of the impact of Hurricane Irma in this coastal ecosystem. Total anoxia that occurred right after the hurricane caused significant mortality of fishes and other aerobic organisms, which were excluded from the lagoon during the following 3 weeks that anoxia lasted. As Patrick *et al.* (2020) have noted, biotic components are likely among the last to recover after a strong hurricane impact. In fact, most studies on hurricane impacts have reported decreases in DO (Gómez-Carro *et al.* 1988; Mallin & Corbett 2006; Chen *et al.* 2017; Kowalski *et al.* 2018), although in some cases, an increase in DO has also been found (Barik *et al.* 2017; Chen *et al.* 2017). Flooding, sediment resuspension and mixing are expected to increase remineralization of organic matter using available DO (Gómez-Carro *et al.* 1988; Peierls *et al.* 2003; Mallin & Corbett 2006), but an enhancement of primary production could also occur (Valiela *et al.* 1998; Peierls *et al.* 2003) and result in an increase in OD. In any case, such an effect is not likely to occur in an already highly eutrophic system like Laguna Larga (González-De Zayas *et al.* 2018), and we did not observe it in this lagoon during 2015–2018.

Eutrophication of Laguna Larga was sustained, during 2015–2017, before the hurricane, by the high concentrations of nutrients – particularly TN, DIN and SRSi – similar to those reported by González-De Zayas *et al.* (2018) for the 2007–2009 sampling period, showing the lagoon remained highly eutrophic. This is a finding similar to those of Chen *et al.* (2017), who reported higher concentrations of nutrients in lagoons with higher urban development in the Gulf of Mexico. Nevertheless, immediately after Hurricane Irma, SRSi, TN, ammonium and DIN increased at the same time as anoxic conditions were reached, showing that a dramatic decrease in the lagoon's water quality was caused by the hurricane. Only phosphorous remained relatively stable as the hurricane passed and then peaked several months later. Around the world, other ecosystems have also experienced mixed responses in nutrient biogeochemistry after storms. Paerl *et al.* (1998) found that all nutrients increased after Hurricane Fran in the Neuse Estuary, and similar responses were found by Reay & Moore (2005), Lin *et al.* (2014) and Chen *et al.* (2017). Hagy *et al.* (2006) reported that all measured nutrients decreased after Hurricane Ivan impacted Pensacola Bay. Barik *et al.* (2017) and Paerl *et al.* (2018) found results similar to those of our study, with some nutrient concentrations increasing and others decreasing.

Opposite to the case of this report on Laguna Larga, most studies on the effects of hurricanes and storms over coastal ecosystems have not followed up on the initial reports of impacts, so that the path of their recovery is not well-known (Galván *et al.* 2012; Barik *et al.* 2017; Chen *et al.* 2017; Paerl *et al.* 2018). Among the few studies that have also evaluated the evolution of coastal ecosystems after hurricane impacts, most followed estuaries and open systems (e.g. Valiela *et al.* 1998; Peierls *et al.* 2003; Kowalski *et al.* 2018), and only two focused on coastal lagoons (Gómez-Carro *et al.* 1988; Kowalski *et al.* 2018), although one of them was centered on salinity changes, and did not consider other parameters critical for water quality, such as DO and nutrients.

In the case of Laguna Larga, our long-term monitoring data, the ANOVA and the PCA suggest that the lagoon had not recovered a water quality similar to what it had before Hurricane Irma until 6 months after the hurricane, by March 2018, with a transition period between November 2017 and January 2018. Similarly, Gómez-Carro *et al.* (1988) concluded that the brackish and polluted lagoon Laguna de la Leche returned to its previous state 5 months after Hurricane Kate in

1985. Kowalski *et al.* (2018) found variable hydrographic recovery times in a Texas Lagoon System, only a month after Hurricane Dolly and 6 months after a more intense cyclone (Hurricane Alex).

In contrast, Valiela *et al.* (1998) found that some measured aquatic parameters as ammonium returned to previous concentrations in a few days after Hurricane Bob on Pamlico Sound. Other reports on estuaries impacted by hurricanes also indicated rapid recovery, but after much lower nutrient peaks than those observed in Laguna Larga (Peierls *et al.* 2003). These, and our results, suggest that the time scale of the recovery not only depends on the intensity of the storm, but also on the resilience of the coastal ecosystem, which depends highly on its water exchange with the surrounding ocean. Another factor decreasing the resilience of lagoons and other coastal ecosystems is the intensity of the anthropic pressure derived from watershed development, mainly through nutrient loading rates, as found by Chen *et al.* (2017) and Deng *et al.* (2021).

In the case of Laguna Larga, the main biogeochemical impact of Hurricane Irma was that it boosted the eutrophic conditions of the lagoon, causing anoxia and higher nutrient concentrations which prevailed for several months. This could not have been detected if the study had not included a follow-up after the hurricane pass, as did our long-term monitoring strategy. Overall, the variability in the responses of coastal systems to extreme weather events found, so far, outlines the need for long-term monitoring of coastal ecosystems, which can give insight and focus on the differential impacts and responses of atrophic vs pristine coastal lagoons and ecosystems.

CONCLUDING REMARKS

Long-term monitoring of Laguna Larga allowed the assessment of the impacts of the passage of Hurricane Irma over the lagoon through a comparison of the changes caused by the hurricane with a previously well-established water quality baseline. Although our monitoring had the limitation of quarterly sampling, immediate intensification of the sampling frequency made possible a detailed follow-up of the impacts on the lagoon.

Our data show that Laguna Larga remained a highly polluted coastal lagoon during 2015–2017, without significant changes in its eutrophic condition as compared to that reported for the 2007–2009 period (González-De Zayas *et al.* 2018).

Hurricane Irma greatly affected most physicochemical parameters in the lagoon, mainly salinity, SRSi, DO and TN, boosting the eutrophic conditions of Launa Larga, and deteriorating the water quality of the lagoon.

The water quality of Laguna Larga did not recover from these impacts until 6 months after the hurricane passed, a time period longer than observed in other systems with less anthropic pressure and/or a stronger communication with the open sea. Both the choked nature of the lagoon and the high atrophic pressure on it made it more vulnerable to the impacts of an extreme event such as Hurricane Irma.

This case study shows the importance of long-term monitoring of coastal ecosystems, which can be key to properly assessing the impacts of unpredictable events, such as a hurricane, in relation to a previously well-established water quality baseline. Long-term monitoring can also be useful to track the impacts of climate change, sea-level rise and other processes affecting our coastal ecosystems. The establishment of long-term monitoring of coastal lagoons and ecosystems throughout the world is therefore highly recommended, particularly for tropical regions, where these extreme events are more likely to occur.

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DATA AVAILABILITY STATEMENT

Data cannot be made publicly available; readers should contact the corresponding author for details.

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