

Effect of extreme climatic events resulting in prolonged precipitation on the reproductive output of sea turtles

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Abstract

Anthropogenic climate change is predicted to increase the variation in storm patterns in some areas in the coming decades. This variation in mean rainfall and increase in mean temperature could increase the extinction risk of species with temperature-dependent sex determination. Taking into account that sea turtle reproductive output depends on climatic conditions, such as precipitation and temperature, extreme climatic events could affect the mortality of eggs and hatchlings. Our main goal was to assess the effects of extreme climatic events resulting in prolonged precipitation episodes on the reproductive output of leatherback turtles *Dermochelys coriacea* and how these events might reduce hatchling production. To study how short periods of protracted rainfall affect leatherback turtle reproductive output, we recorded (1) the hatching success of $n = 48$ nests located at 50, 75 and 90 cm depths under sun and shaded treatments from 2013 to 2015 at the Pacuare Reserve in Caribbean coast of Costa Rica, (2) the water table level and (3) sand moisture at 10, 25, 50, 75 and 100 cm depths. In addition, we assessed changes in seasonal precipitation, nest abundance and the annual hatching success of leatherbacks over time. The results show that prolonged precipitation significantly influenced hatching success. Protracted rainfall increased the water table levels and sand moisture in some places, which consequently increased egg mortality in deeper nests. These effects may be higher considering the expected increase in storm frequency. Thus, the assessment of the effects of these extreme events on nesting grounds is necessary to predict the potential extinction risk of sea turtle populations.

Introduction

Changes in climate of potential anthropogenic origin are predicted to increase the variation in storm patterns and cause more intense and frequent precipitation in the upcoming decades (IPCC, 2013). These variations in mean rainfall and mean temperature could affect the extinction risk in species exhibiting temperature-dependent sex determination. The effects of climate change may vary among locations, and some populations might be more affected than others (Fernández-Chacón *et al.*, 2011; Wernberg *et al.*, 2012; Santidrián Tomillo *et al.*, 2015a, 2015b; Butt, Whiting & Dethmers, 2016). Climate variability will depend on changes between strong El Niño–Southern Oscillation years (ENSO) and non-El Niño years in the Caribbean region (Reguero, Méndez & Losada, 2013).

The nesting grounds of sea turtles are mainly located in the tropical and subtropical areas, which are highly influenced by variable climatic conditions among seasons, such

as the ENSO (Santidrián Tomillo *et al.*, 2014) and the North Atlantic Oscillation (NAO) (Ottersen *et al.*, 2001), which represent the dominant climate pattern in the North Atlantic region (Hurrell *et al.*, 2003; Stenseth *et al.*, 2003). Taking into account that female reproductive output depends on climatic conditions, such as temperature (Matsuzawa *et al.*, 2002; Santidrián Tomillo *et al.*, 2012, 2015a,b; Pike, Roznik & Bell, 2015) and precipitation (Houghton *et al.*, 2007; Saba *et al.*, 2012), extreme climatic events might affect the mortality of nests. Thus, microhabitat variations due to locally heavy and prolonged rainfall (Standora & Spotila, 1985) will affect nest microhabitat features (Wyneken & Lolavar, 2015) and consequently reproductive output, even when female turtles lay a high number of clutches within a reproductive season, which should buffer the effects of local climatic variations (Hays *et al.*, 2001).

Sea turtles are a species in which sex determination is temperature dependent (Mrosovsky & Pieau, 1991). Hence,

increasing temperatures cause female-biased sex ratios (Godfrey, Mrosovsky & Barreto, 1996; Fuentes *et al.*, 2009; Hawkes *et al.*, 2009; Woolgar, Trocini & Mitchell, 2013) and the mortality of eggs and hatchlings (Santidrián Tomillo *et al.*, 2012, 2014). Increases in temperature are predicted to decrease hatchling success in tropical locations more than in temperate areas (Pike, 2014; Pike *et al.*, 2015). Other environmental effects, such as protracted precipitation and moisture, might also affect the sexual determination and mortality of embryos within the nest. Furthermore, the temperature during incubation will also depend on nest depth and shade (Patiño-Martínez *et al.*, 2012; Jourdan & Fuentes, 2013; Wynneken & Lolavar, 2015), and precipitation could mitigate the effects of high temperatures by cooling the nests (Houghton *et al.*, 2007).

Climatic models predict more extreme weather and more frequent heavy precipitation events in wet tropical regions than in others in coming decades due to the increased frequency of intense tropical cyclone activity (IPCC, 2013). Thus, further research focused on studying the effects of these climatic alterations is needed to predict how they might affect the hatching success of sea turtle species, such as leatherbacks *Dermochelys coriacea*.

Increasing temperatures reduce the reproductive output of leatherbacks (Patiño-Martínez *et al.*, 2012; Santidrián Tomillo *et al.*, 2014) as well as precipitation accumulated over time (Santidrián Tomillo *et al.*, 2015a,b). However, the effects of prolonged precipitation events with strong rains during consecutive days on leatherback hatching success are still unknown and could not be highlighted by monthly averages. Protracted precipitation might rise water table levels and consequently, sand moisture, which must affect hatching success. Considering that the hatching success of this species is the lowest among all sea turtle species (Rivas, Fernandez & Marco, 2016b), this threat might result in population decline.

Our main goal was to assess the effects of protracted precipitation periods on the reproductive output of leatherback turtles. The objectives of this study were to record (1) the effect of precipitation on the reproductive output of *Dermochelys coriacea* based on shaded and non-shaded treatments and nest depth, (2) changes in sand moisture with depth and (3) variations in the water table level at three sites along the beach throughout the season. In this way, our study can clarify the potential effects of extreme climatic events on leatherback species, which might contribute to predict the extinction risk of other populations under future scenarios of climate change.

Materials and methods

Study site

The study was conducted at Pacuare Beach (5.7 km) in the Pacuare Nature Reserve (PNR) located on the Caribbean coast of Costa Rica. The Reserve's limits are 10°13'17"N, 83°16'39"W and 10°10'00" N, 83°14'00" W. To record nest locations, the length of the beach was marked into sectors and the width into three zones: the intertidal zone (zone A), the high beach zone above the high tide line (zone B) and close to the vegetation (zone C).

A stable nesting population of leatherback turtles nests at PNR every season from March to July, with the nesting peak occurring in April and May (Rivas *et al.*, 2016a). We included data obtained from a 2000 monitoring project, such as the number of *in situ*, relocated nests and nest depth, which were recorded during the excavation process, and hatching success 2 days after hatchling emergence, to determine averages. Hatching success was calculated as the proportion of eggs that produced hatchlings: $H = S/(S + U)$, where S = number of eggshells and U = number of unhatched eggs. Eggshell fragments $\geq 50\%$ of the egg surface were considered to be one hatched egg (Miller, 1999).

Precipitation and air temperature data were obtained from the Limón Weather Station located at the Limón airport (~38 km from PNR) from the National Meteorological Institute of Costa Rica (IMN, 2014). The monthly accumulated precipitation average was also calculated for the study period.

Experimental treatments – sun exposure and depth

To determine the effects of sun exposure, nest depth, local temperature and local precipitation on hatching success, we relocated 48 nests per year to a beach hatchery during the nesting seasons in 2013, 2014 and 2015. The hatchery was located close to the primary vegetation, and its dimensions were 10 × 8 m on a 0° slope, delimited by a trough 1 m in depth and a fence 1 m in height. Half of the hatchery (10 × 4 m) was shaded, and half was sun-exposed. We used a black material to create shade, allowing 40% sun radiation at 1.5 m above the sand. Nests were placed at three depth treatments at 50, 75 and 90 cm of depth in a block design considering the depth range of *in situ* nests at PNR (mean \pm SD) (74.6 \pm 7.2). We tested eight nests per depth under each of the sun exposure treatments. Temperature loggers were buried to record incubation temperature per treatment, but results were not included in this study because some loggers failed and others were buried in nests that did not hatch.

Clutches were relocated to the hatchery every night following female oviposition and were randomly allocated to sun or shade exposure. The maximum distance of transportation was 800 m within an hour after laying. Every nest form was removed by digging in a similar way; however, because 90-cm nests are difficult to remove by hand, a shovel was used to reach the bottom. The nests were covered with sand in the same order that they were removed to maintain the original level of sand moisture. The nests were excavated 2 days after hatching to determine hatching success, which was estimated as the proportion of eggs in a clutch that produced hatchlings. The incubation period was considered as the number of days elapsed between egg burial and the emergence of the first hatchling.

Sand moisture and water table level

After persistent precipitation events in 2014, we recorded the sand moisture at three equidistant sites in zone B in 2015 to cover the entire beach: site (1) was close to the southern

reserve limit and next to the hatchery, site (2) was in the middle of the beach, and site (3) was in the northern part of the reserve. The sand was collected at the same location at 0600 h on the same day in April, May, June and July 2015. Over 20 g was collected at every site from depths of 10, 25, 50, 75 and 100 cm to include the range of egg locations in *in situ* nests at PNR. Samples were placed in a Ziploc bag with the air removed to avoid moisture loss in transit to the Soil, Plant and Water Lab at the Earth University. The 20-g samples were weighed in under 4 hours after collection to the nearest 0.1 g and dried to a constant mass for 72 hours at 105°C. The moisture content was calculated as the ratio of water loss to dry mass (humid mass – dry mass/dry mass) multiplied by 100 (Head, 1992).

To record water table variations, we used a PVC tube, 2” diameter and 1.20 m long, buried at 1 m depths at the same three sites selected in zone B (where the sand samples were collected). We fixed a microfibre net to the end of the tube in contact with the sand to prevent sand filtration into the tube and a tap with holes covering the other end of the tube to prevent the inclusion of rain in the measurements. The water level was recorded using a PVC tube that was 1” and 1.40 m long. Measurements were recorded in centimetres from the bottom of the tube and were taken once a week.

Statistical analysis

A generalized linear model (GLM) analysis was performed to compare (1) the number of nests among months and years, (2) precipitation among months and years, (3) the effects of the shaded and non-shaded treatments by depth on hatching success among years, (4) sand moisture among sites, depths and months, and (5) water table level among sites, days and months. A one-way ANOVA and Tukey’s post-hoc test were used to test differences in air temperature among months and depths under the sun exposure and depth treatments. The Kruskal–Wallis test was used to compare hatching success among sectors along the beach. Linear regression was used to estimate the trend in hatching success over the years. We used the Jaguar library and R commander in R, version 3.2.1. (R Core Team, 2015) and STATISTICA v. 7.0 (StatSoft, Inc. Tulsa, USA).

Results

Nesting trends

We recorded the highest numbers of nests at PNR in April (mean \pm sd) (274.9 \pm 89.2) and May (280.9 \pm 83.3) from 2000 to 2015. The GLM model was significant among months ($F = 16.03$, $P < 0.001$) (Fig. 1) but not among years ($F = 0.82$, $P = 0.64$) except 2009–2013 and 2012–2013 ($P = 0.04$). A mean of 33.51 \pm 9.27% of all the nests laid in PNR were relocated to safety zones B–C from 2010 to 2015. The mean depth nesting females dug to lay their clutch from 2010 to 2015 was \sim 76.9 \pm 2.5 cm. The hatching success did not vary significantly among sectors along the beach (Kruskal–Wallis test, $H = 219.8$, d.f. = 194, $P = 0.10$).

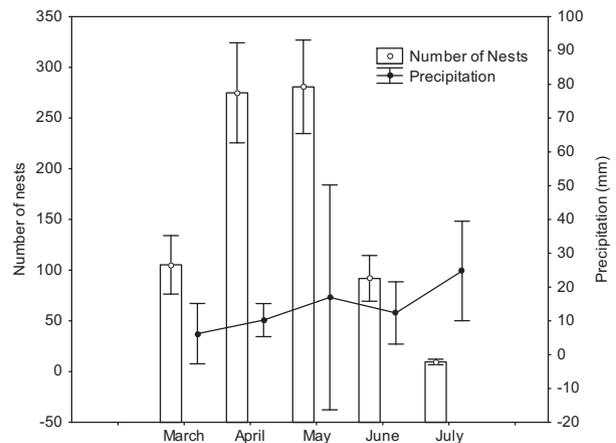


Figure 1 Number of nests laid by leatherback turtles *Dermochelys coriacea* from 2000 to 2015 and precipitation (mm) recorded between 2013–2015. The centre point in the box represents the mean value; the whiskers represent the confidence interval.

Environmental trends

The GLM test for precipitation was not significant for months \times years ($F = 17.3$, $P = 0.04$), but it was significant among months ($F = 29.64$, $P < 0.001$). The highest monthly precipitation variation from 2013 to 2015 was in May (SD = 13.4 mm), with means of 9.1, 9.3 and 32.41 mm respectively (Fig. 1). The seasonal precipitation showed the highest 1-month moving average in July in 2013 and 2014 and in May in 2015 (Fig. 2). The post hoc test identified differences in May in 2015 ($F = 3.0$, $P = 0.002$) (Fig. 2). There was only a single day in May 2015 where the mean daily precipitation more than 250 mm. Precipitation in July 2013 affected only one nest at the hatchery, but protracted precipitation affected more than eight nests in mid-July 2014 and more than the half of the hatchery in May 2015. The mean air temperature during the study period was 25.8 \pm 0.98°C (range: 25.74–25.87°C), and it differed significantly among years ($F = 805.3$, d.f. = 940, $P < 0.001$) (Fig. 3).

Hatchery treatments

Considering the effects of sun and shade conditions, depth and year, the highest mean hatching success was recorded at 50 cm depth in 2013 and the lowest at 90 cm in 2015 under the shade treatment (Fig. 4). Eight of 18 nests at 75 and 90 cm depth did not hatch after rains in 2014, and neither did over half of the total number of nests (22 of 48 nests) at the same depths in 2015.

We found significant differences in hatching success among depths, years and shading treatments among years (Table 1). The Tukey’s post-hoc analysis showed differences in hatching success among nests at 50 cm depth (independent of shading treatment), between shading treatments for those constructed at 50 cm depth, and among nests constructed in 2015. The mean hatching success decreased significantly over the 3 years ($F = 14.56$, $P < 0.0001$). Nests at

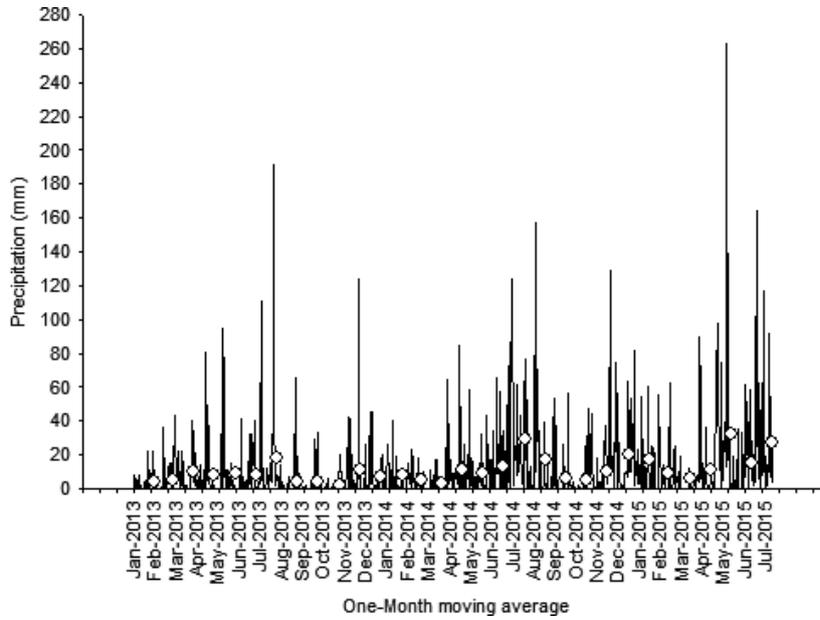


Figure 2 Mean monthly precipitation (mm) in the Caribbean region of Costa Rica from 2013 to 2014. Data were smoothed with a 1-month moving average and are represented with white points.

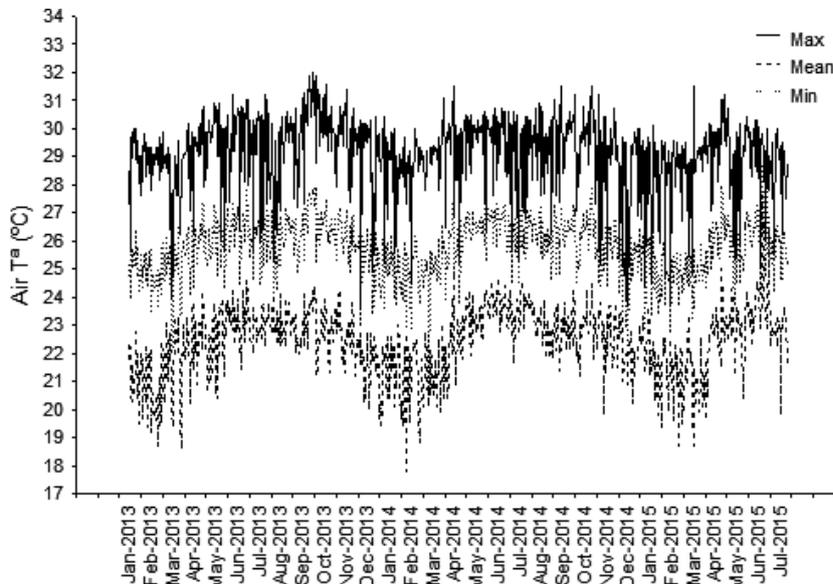


Figure 3 Air temperature recorded (°C) in the Caribbean region of Costa Rica from 2013 to 2015. Maximum, mean and minimum are represented by a continuous line and dashed lines.

90 cm depth showed the lowest hatching success over the study period ($F = 25.15, P < 0.0001$) (Fig. 4).

Sand moisture and water table level

The general linear model showed significant differences in sand moisture among months ($F = 39.5, P < 0.001$) and for the interaction between month and depth ($F = 45.1, P < 0.001$), but no differences were found among sites

($F = 0.52, P = 0.77$) or depths ($F(4,55) = 1.06, P = 0.39$) (Fig. 5). The Tukey’s post-hoc analysis showed significant differences among all months except for April and June ($F = -0.85, P = 0.40$) and April and July ($F = 1.85, P = 0.06$) (Table 2) and significant differences between 75 ($F = 3.58, P < 0.001$) and 100 cm depths in May at site 1 ($F = 4.4, P < 0.001$) (Fig. 5).

The general linear model showed differences in water table levels among sites ($F = 14.53, d.f. = 2, P < 0.0001$)

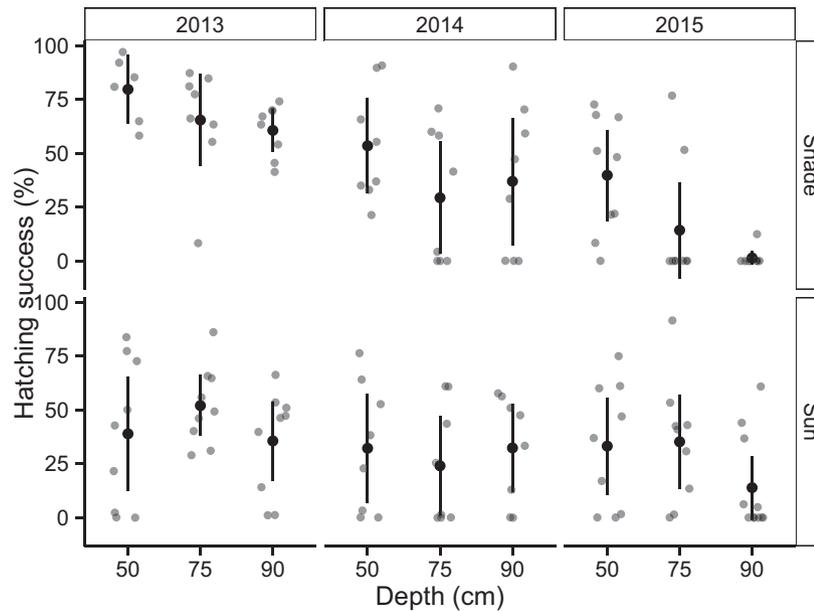


Figure 4 Hatching success (%) of leatherback turtle nests under sun and shade treatments and different depths (50, 75 and 90 cm) in 2013, 2014 and 2015. The centre point in the box represents the mean value; the whiskers represent the confidence interval.

Table 1 Generalized linear model (GLM) results on the effects of depth, shading and year on the hatching success of leatherback turtle nests located in the hatchery during the study period

Factor	d.f.	<i>F</i>	<i>P</i>
Depth	2	10.13	0.006
Shading	1	3.7	0.054
Year	2	38.98	0.000
Depth × shading	2	5.51	0.063
Depth × year	4	6.07	0.194
Shading × year	2	12.02	0.002
Depth × shading × year	4	0.35	0.985

Significant values are in bold.

and months ($F = 22.28$, d.f. = 4, $P < 0.0001$) but not among days ($F = 154.92$, d.f. = 128, $P = 0.053$). The Tukey's post hoc analysis showed significant differences in May between sites 1–2 ($F = -4.7$, $P < 0.001$) and among sites 1–3 ($F = -4.3$, $P < 0.001$) (Fig. 6). May was the only month with a persistent water table level during 6 consecutive days at site 1; the mean was 42.25 ± 12 cm. The persistence of a water table level of more than 10 cm at the other two sites did not exceed 1 day.

Discussion

Heavy rainfall in the wet-dry tropics modifies not only hydric conditions in the soil but also temperatures, causing a significant and rapid drop in mean temperatures (Shine & Brown, 2008). Wyneken & Lolavar in 2015 observed that the effects of both factors on reproductive output are especially pronounced when high moisture levels interact with extremely warm incubation. A recent study also showed

temperatures impact both hatching success and sex ratio (Hays *et al.*, 2017).

However, as Paukstis, Gutzke & Packard (1984) found, the mean seasonal air temperatures recorded at PNR highlighted that temperature alone does not accurately predict turtle sex ratios or hatching production because the hydric environment also influences the mortality of embryos. Hence, precipitation (Houghton *et al.*, 2007) and inundation caused by sea-level rise (Pike *et al.*, 2015) might also play important roles in embryo mortality, but their influences on incubation features and hatching success are poorly understood.

Many studies have been using IPCC predictions for future climate change with a focus on temperature (Laloë *et al.*, 2014) but changes in rainfall might also be assessed considering that this study shows that extreme climatic events of precipitation with a protracted duration of less than a week significantly decrease hatching success, affecting every deep nest. Taking into account the relationships among the analysed variables in this study at PNR, it could be highlighted that the influences of extreme climate events are not shown in annual averages. Consequently, we consider that annual mean precipitation used by IPCC predictions (IPCC, 2013) might not be an accurate predictor to assess the effect of precipitation on total reproductive output because the frequency and intensity of those episodes were not shown in the seasonal mean data, but might have important implications for predictive models of climate change (Wernberg *et al.*, 2012). Thus, the estimation of monthly averages might provide more reliable predictions to assess the impact of this factor on annual production.

At certain sites rainfall is rare [e.g. Cape Verde (Laloë *et al.*, 2014), Saint Croix and South Africa (Santidrian *et al.* 2015a,b)] and at other sites with high rainfalls, such as

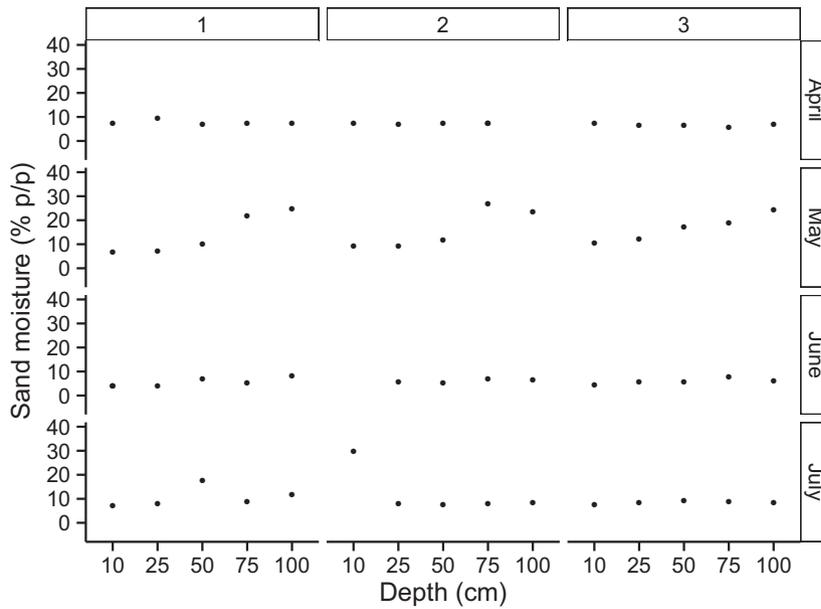


Figure 5 Sand moisture (% p/p) recorded at 10, 25, 50, 75, 100 cm depths at sites 1, 2 and 3. The point in the box represents the mean value.

Table 2 Tukey’s post hoc test results for sand moisture measurements collected from three sectors along the beach (sites 1, 2 and 3) among months.

	SE	z value	P
Site 1	2.21	3.50	<0.001
Site 2	3.13	-0.11	0.910
Site 3	3.13	-0.37	0.716
July	3.13	0.89	0.380
June	3.13	-0.65	0.522
May	3.13	2.02	0.048
Site 2 – July	4.43	0.48	0.631
Site 3 – July	4.43	-0.19	0.847
Site 2 – June	4.43	0.08	0.939
Site 3 – June	4.43	0.29	0.772
Site 2 – May	4.43	0.53	0.595
Site 3 – May	4.43	0.81	0.421
April–May	1.74	4.80	<0.001
April–June	1.74	-0.85	0.4
April–July	1.74	1.85	0.065
May–June	1.74	5.65	<0.001
May–July	1.74	2.95	0.003
June–July	1.74	-2.7	0.007

Significant values are in bold.

tropical sites, should be further studied (Godfrey *et al.*, 1996; Esteban *et al.*, 2016). At PNR, we observed that if protracted rainfall events are frequent during the seasonal nesting peak in May–July, the annual reproductive output could be affected by the massive mortality of eggs. Since the timing and intensity of rainfall events are difficult to predict and because both the intensity and duration of storm events have increased since the 1990s (Webster *et al.*, 2005; IPCC, 2013), we could expect variation throughout every

nesting season. The seasonal time at which clutches are laid could be affected, regardless of whether increased storminess results in changes in rainfall patterns or whether storms are more frequent in the future. The ultimate effects of these events will also depend on slight variations in the seasonal timing of nesting (Pike & Stiner, 2007). The identification of the effects of the key ecological abiotic variable of rainfall might lead to the implementation of effective measures to protect this and other threatened species (Dawson *et al.*, 2011).

Conservation implications

Excessive precipitation and flooding at the beach, such as the presence of dune scarps, negatively influence female nesting behaviour, increasing the number of nests laid in over-flooded zones (Rivas *et al.*, 2016b, c) or pushing females to lay in areas where nests will be affected by the presence of dune plants (Rivas & Marco, 2016c). However, the moisture content and salinity of the surface sand are not potential cues for nest site selection because they can vary depending on rainfall and water table changes (Wood & Bjorndal, 2000). To avoid doomed eggs, an important number of nests at PNR and other nesting sites are relocated to zones B–C, where water table level changes are common. The use of doomed-egg relocation does not significantly change the gene pool (Pfaller, Limpus & Bjorndal, 2008) and might be one of the main management strategies in the future. However, based on our results, the microhabitat conditions where egg emplacement occurs will determine the reproductive output and sex ratio (Fuentes, Fish & Maynard, 2012). Therefore, to assess the optimum incubation conditions, abiotic factors, such as precipitation, water table levels and temperature, it should be assessed prior to

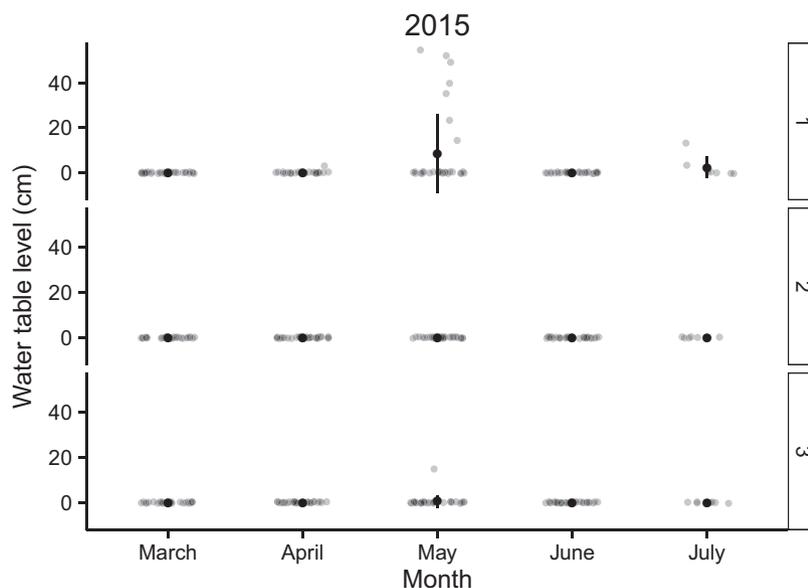


Figure 6 Water table level measurements (cm) recorded once a week at sites 1, 2 and 3 in March, April, May, June and July in 2015. The center point in the box represents the mean value; the whiskers represent the confidence interval.

the implementation of any management strategies. In summary, local long-term studies could help in the understanding of whether changing climatic patterns, such as increasing storm frequency, could threaten nesting sea turtle populations in the future.

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