




The impacts of extreme El Niño events on sea turtle nesting populations

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Abstract

The El Niño Southern Oscillation (ENSO) is the predominant interannual pattern of climate variability in the world and may become extreme approximately once every 20 years. Climate-forced interannual variability in fecundity rates of long-lived species are well-studied, but the effect of extreme events is less clear. Here, we analyzed the effect of the extreme 2015–16 El Niño event on three long-lived sea turtle species in a region highly influenced by ENSO. The effect of this extreme event varied considerably among species. While reproductive success dramatically declined in leatherback turtles (*Dermochelys coriacea*), the reduction was only marginal in green turtles (*Chelonia mydas*). Nevertheless, the number of nesting green turtles decreased following the extreme El Niño event, likely due to decreased ocean productivity. We used global climate models to project an increase in the decadal occurrence of extreme events from ~0.7 events (beginning of twentieth century) to ~2.9 events per decade (end of twenty-first century). This resulted in a projected decline in the reproductive success of leatherback turtles (~19%), a milder decline in olive ridley turtles (*Lepidochelys olivacea*) (~7%), and no decline in green turtles (~1%). Extreme El Niño events can have a strong detrimental effect on East Pacific leatherback turtles, a population that is already critically endangered due to other anthropogenic impacts. Our results highlight the importance of conducting species-specific and site-specific analyses of climatic impacts on sea turtles.

Keywords ENSO · Extreme events · Long-lived · Sea turtles · Reproductive success · Climate change

1 Introduction

Global and regional impacts driven by El Niño Southern Oscillation include changes in air temperatures, trade winds, storm activity, and precipitation patterns that can affect wildlife,

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ecological processes, and local economies (Stenseth et al. 2002; Wolter and Timlin 2011; Cai et al. 2015; Philander 1983). It results from the interactions between the atmosphere and the ocean and is characterized by relative unpredictability (Rasmusson and Wallace 1983), alternating from an El Niño phase, characterized by increased ocean temperature and decreased ocean productivity throughout the eastern Pacific Ocean, and a La Niña phase, when the contrary is true (Chavez et al. 1999).

The natural variability of El Niño Southern Oscillation (ENSO) can occasionally lead to extreme events, such as those occurring in 1982–1983 and 1997–1998. Extreme El Niño events have the potential to cause droughts, fires and floods, damaging ecosystems, agriculture, and fisheries (Cai et al. 2014, 2015; Santoso et al. 2017). For instance, the extreme El Niño event of 1997–1998, considered “the climatic event of the century,” cost billions of US dollars in damage (Cai et al. 2014). Because of its devastating effects on the economy and nature, the relationship between extreme El Niño events and greenhouse gas emissions has received considerable attention in recent years (Cai et al. 2014; Wang et al. 2017). One particular study determined that the frequency of extreme events would increase along with global mean temperatures and double if temperatures rose to the target of 1.5 °C above pre-industrial levels that was set at the Paris Agreement (Wang et al. 2017), which is still considered a moderate climate change scenario (IPCC 2013).

The first extreme El Niño event of the twenty-first century occurred in 2015–16 and its effects were felt worldwide. Extreme droughts and fires were recorded in the northern Brazilian Amazon (Fonseca et al. 2017), substantial beach erosion effected the Northwest coast of the US (Barnard et al. 2017) and floods occurred in Peru (Santoso et al. 2017). The severity of the 2015–16 event was also exacerbated by the unusually warm conditions registered during 2014 (Santoso et al. 2017). The North Pacific region of Costa Rica suffered a severe drought during this time as rainfall there is associated with ENSO (Waylen et al. 1996). North Pacific Costa Rica has a distinctive climate from the rest of the country that is characterized by a rainy season from June to October (with September and October as the rainiest months), followed by a dramatic dry season between December and April (being May and November as transition months). Dry conditions are aggravated during El Niño years causing severe droughts (Waylen et al. 1996) and damaging the local economy, which is largely based on cattle production and therefore, dependent on precipitation levels (Retana and Rosales 2000).

Climate-forced inter-annual variability in fecundity rates is common among long-lived species (Gaillard et al. 1998), but the effect of extreme events has been less studied. Based on number of nesting females, Costa Rica is among the most important regions for sea turtles in the Americas, and it holds nesting populations for all but two of the seven sea turtle species found worldwide. Four species nest in the North Pacific region and three of them, leatherback turtles (*Dermodochelys coriacea*), green turtles (*Chelonia mydas*), and olive ridley turtles (*Lepidochelys olivacea*), have significant rookeries, among the most important in the region. In the case of the leatherback turtle, which is critically endangered in the eastern Pacific (Wallace et al. 2013), it has been previously determined to be affected by ENSO. Their fecundity is reduced during dry and warm El Niño years by means of decreased reproductive frequency (Saba et al. 2007) and hatching success (Santidrián Tomillo et al. 2012). Because of the effect of local climate on hatching success, population declines will likely follow under continued climate change (Saba et al. 2012). The effect of ENSO on the other sea turtle populations that use this same region, as well as the potential impact of extreme events on all of them, remain unknown. However, similar impacts could be expected because egg clutches

of different species incubate on the same beaches and they all forage in regions of ENSO influence. Leatherback turtles mainly forage on gelatinous zooplankton such as jellyfish in the tropical Pacific (Saba et al. 2008), green turtles on seagrass and algae in coastal areas (Seminoff et al. 2002) and olive ridley turtles are omnivorous, eating a wide range of prey such as crabs, salps, algae, or fish, and can have wide dispersions (Plotkin et al. 1995; Spotila 2004). Given that the eastern tropical Pacific is an area of high influence by ENSO, where the three species are found, we would expect that population declines under increasing frequencies of extreme events, even if other anthropogenic impacts were reverted. The objective of this study was to assess the effect of extreme El Niño events on three different species of sea turtles that nest in Northwest Costa Rica, an area highly influenced by ENSO.

2 Methods

The beaches with the highest abundance of nesting turtles in Pacific Costa Rica are located in the Nicoya Peninsula, Northwest Costa Rica. We obtained information on nesting abundance and reproductive success for three sea turtle species, leatherback (*Dc*), green (*Cm*), and olive ridley turtles (*Lo*) that nest in this area (Table 1). From North to South, these beaches were (species that nest on each beach in brackets) San José Island (*Cm*), Nancite (*Cm*, *Lo*), Cabuyal (*Cm*, *Lo*), Playa Grande (*Dc*, *Lo*), Punta Pargos (*Cm*), and Ostional (*Lo*). Olive ridley *arribadas* occur at Nancite and Ostional. *Arribadas* are synchronic mass nesting events that last a few nights, take place approximately once per month and only happen in a few places worldwide (Fonseca et al. 2009; Valverde et al. 2012). The rest of beaches hosted solitary nesters. For each species, we included nesting beaches that were either considered index (main beaches) or secondary sites depending on the number of nesting turtles and their regional relevance (Santidrián Tomillo et al. 2017a). Thus, a beach could be classified as index beach for a species and secondary for another. Index sites (species in brackets) included San José Island (*Cm*), Cabuyal (*Cm*), Nancite (*Lo*), Ostional (*Lo*), and Playa Grande (*Dc*). Secondary beaches included Nancite (*Cm*), Punta Pargos (*Cm*), Cabuyal (*Lo*), and Playa Grande (*Lo*) (Table 1). Playa Grande (together with the two other smaller beaches that comprise Las Baulas National Park) is the only index site for leatherback turtles in Costa Rica. Because the number

Table 1 Nesting beaches by species, type of beach, and proxy of nesting abundance. All beaches were located in North Pacific Costa Rica and were important nesting sites for the three species that are regular nesters in this area. Type of nesting beach was either index or secondary beach. Proxy for nesting abundance was nests, body pits, and/or females. *nesting beaches where *arribadas* occur

Beach	Species	Beach type	Proxy nesting abundance
Nancite*	<i>L. olivacea</i>	Index	Nests
Cabuyal	<i>L. olivacea</i>	Secondary	Body pits
Playa Grande	<i>L. olivacea</i>	Secondary	Body pits
Ostional*	<i>L. olivacea</i>	Index	Nests
Isla San José	<i>C. mydas</i>	Index	Nests
Nancite	<i>C. mydas</i>	Secondary	Nests
Cabuyal	<i>C. mydas</i>	Index	Nests, females
Punta Pargos	<i>C. mydas</i>	Secondary	Nests
Playa Grande	<i>D. coriacea</i>	Index	Body pits, females

of leatherback turtles at secondary beaches is now very low (~3–5 females per year, Santidrián Tomillo et al. 2017a), we did not include any other beach for this species.

2.1 Nesting abundance

Depending on the methodology followed by each monitoring project on each of the study beaches, we used either the number of body pits, nesting females, and/or nests as indicators of nesting abundance, choosing the most reliable estimation in each case (Table 1). We used nesting females as proxy of nesting abundance when beach effort was high and thus all females were likely seen in a season (as they nest multiple times, the probability of missing a turtle every time she nests in a given nesting season is very low when beach coverage is high). Alternatively, when efforts were more directed towards verifying all egg laying than identifying individual females, we used the number of nests. Finally, we used body pits when both the number of females and nests was likely underestimated (i.e., olive ridley turtles at Playa Grande are likely to be missed for the season if they are missed just one time, as most turtles lay only one clutch per nesting season). In this case, all body pits were counted but not necessarily all turtles and nests, as some females were not seen and/or not all egg laying events were verified. The number of nests registered at the *arribadas* at Ostional and Nancite was estimated using the methodology of transects (Gates et al. 1996). We calculated the annual number of females, nests, and/or body pits at each site between October and February (months of the nesting season) for green, leatherback, and solitary olive ridley nesting beaches. Olive ridley solitary nesters also tend to nest outside of that time frame, but the core of nesting activity still coincides with that of the other species. Nevertheless, the nesting period at the *arribada* beaches is slightly different as these events may occur year-round. For Ostional, we included data on nesting abundance between July of 1 year to June of the next and for Nancite, between July of 1 year to February of the next (since there are no *arribadas* there between March and June). Because the proxy used to measure nesting abundance varied between sites, we compared nesting trends but not numbers between locations.

We used the multivariate ENSO index (MEI) as an indicator of the strength of El Niño events and compared it to nesting abundance. We used mean MEI values for the same year (January–December) of the nesting season (MEI_{current}), for the year before (MEI-1), for 2 years before (MEI-2), and for 3 years before (MEI-3), because sea turtles normally migrate to the nesting beach every 2–4 years (Saba et al. 2007). The MEI data were available at <https://www.esrl.noaa.gov/psd/enso/mei/>.

2.2 Reproductive success

We used hatching success (percentage of eggs that hatch in a clutch) as an indicator of reproductive success and estimated it following the formula $H = S/(S + U)$, where S corresponded to the number of eggshells left by hatchlings that hatched successfully from the egg and U corresponded to the number of unhatched eggs. Eggshells were only counted as one egg when at least 50% of the shell remained (Miller 1999). We estimated annual hatching success for each species at each beach using the mean value for all clutches laid over a nesting season as defined above. We included data from clutches laid between July and February for both *arribada* nesting beaches. Although *arribadas* in Ostional can occur throughout the year, these are typically very small during the dry season and with no hatchling production due to hot and dry conditions. Therefore, data was not available from February onward. In addition,

we did not use hatching success data for the green turtles of Nancite and Punta Pargos, as the sample size was too low in Nancite (not determined for 2 years) and all clutches were relocated at Punta Pargos due to a high risk of being poached and therefore, did not incubate in natural conditions. To compare hatching success with local climatic conditions, we obtained local climate data (air temperature and precipitation) from a nearby weather station at the Liberia airport (< 70 km from all nesting sites), Northwest Costa Rica, facilitated by the National Meteorological Institute of Costa Rica. We used the MEI values (MEI_{rainy}) that corresponded to the months of the rainy season in Northwest Costa Rica (May through October), as precipitation is influenced by ENSO and it has been shown that it greatly affects hatching success of leatherback turtles in this area (Santidrián Tomillo et al. 2012).

2.3 Projections of the effect of extreme events on reproductive success

We considered that an El Niño event became extreme when the average austral summer rainfall was greater than 5 mm/day as defined in previous studies (Cai et al. 2014). We used historical output (years 1850–2005) and the Intergovernmental Panel on Climate Change (IPCC) Representative Concentration Pathway RCP8.5 projections from 6 global climate models (CanEMS2, CESM_CAM5, CNRM-CM5, GFDL_CM3, GISS-E2-H, and MRI_CGCM3) that resolve present-day ENSO dynamics and feedbacks (Wang et al. 2017) from the Coupled Model Intercomparison Project Phase 5 (CMIP5). The datasets were accessed from the Earth System Grid Federation (ESGF) at <https://esgf-node.llnl.gov/projects/esgf-llnl/>. We determined the occurrence of extreme events for each model between 1850 and 2100 and calculated the average number of events over particular time periods to detect changes in frequency.

To assess how the frequency of extreme events affects the reproductive success of the turtles, we calculated reproductive success as the mean annual production of hatchlings over a decade considering the frequency of extreme events projected by the global climate models for that time frame. Then, we compared the mean reproductive success of turtles nesting on the second half of the nineteenth century and first and second half of the twentieth and twenty-first centuries. The annual production of hatchlings was estimated for each species using the following formula:

$$AH = ECF \times cs \times (f_1(H_1) + f_2(H_2))$$

where AH was the mean annual production of hatchlings, *ECF* corresponded to the mean estimated clutch frequency (number of clutches laid in a season) for the nesting population (estimated as the mean ECF of all turtles for which it has been estimated), *cs* to the clutch size (mean number of eggs in a clutch), f_1 and f_2 to the frequencies of extreme and regular ENSO years, respectively, over a decade, and H_1 and H_2 to hatching success under extreme and regular ENSO conditions, respectively. Mean (\pm SD) clutch size and ECF were obtained from the long-term monitoring project at Playa Grande for leatherback turtles (66 ± 16.6 eggs and 6.1 ± 3.1 clutches, respectively) and from published articles available for the area for green (76.9 ± 18.2 eggs and 4.3 ± 2.3 clutches) (Santidrián Tomillo et al. 2015a) and olive ridley turtles (87.5 ± 33.6 eggs and 2.2 ± 1.1 clutches) (Van Buskirk and Crowder 1994; Dornfeld et al. 2015). Values of *ECF*, *cs*, and H_1 were obtained by randomly picking one value within the standard deviation of their mean to account for natural stochasticity. We ran the model 100,000 times using the

function r_{norm} in R and averaged the resulting values. For H_2 , we used the standard deviation corresponding to years with regular ENSO conditions.

2.4 Statistical analyses

We used R version 3.5.0 (R Core Team 2018) and Statistical Package for Social Sciences (SPSS) version 24 (IBM Corp 2016) to conduct statistical analyses. We detrended nesting abundance time series for each beach using the detrended function of the practical numerical math functions (PRACMA) package in R and used Pearson correlations to compare detrended values to the MEI values (MEI_{current}, MEI-1, MEI-2, and MEI-3). We used the Shapiro-Wilk test to assess for normality in the distributions of nesting abundance. Finally, we tested for possible autocorrelation between years in nesting abundance on the detrended time-series and the actual values using the autocorrelation function (ACF) in R. We used SPSS to run Pearson correlations between MEI and local climatic conditions and linear regressions to test the effect of MEI on hatching success.

3 Results

Local climatic conditions were correlated with the MEI during the months of the rainy season, both with (1) precipitation accumulated ($r = -0.689$, $P < 0.01$, $n = 39$ years) and (2) air temperature ($^{\circ}\text{C}$) over the same time period ($r = 0.649$, $P < 0.01$, $n = 39$ years). The 2015–16 El Niño event greatly influenced local climatic conditions in northern Costa Rica, being the hottest and driest year since registers started in 1976. This means that despite being of lower intensity than the 1997–98 El Niño extreme event, the influence of the 2015–16 event on local climate was larger, surpassing all previous records (Fig. 1). Additionally, the extremely hot and dry conditions registered in 2014 (Fig. 1) likely exacerbated the impact of the 2015–16 El Niño event in this area.

Although there was some level of autocorrelation among years in the nesting abundance of each species and site, this was not statistically significant for any time-series ($P > 0.05$ all cases). We did not find a general effect of ENSO on nesting abundance in leatherback, green, or olive ridley turtles when comparing MEI values to the detrended nesting values ($P > 0.05$ all cases). Nesting abundance of green turtles was low during the El Niño event (2015–16) and lower during the year after (2016–17), and was followed by an increase in 2017–18 (Fig. 2). The same trend was found in all green turtle nesting beaches and the numbers were highly correlated among beaches ($P < 0.05$ all cases). Nesting abundance of olive ridley turtles appeared unaffected by the 2015–16 event (Fig. 2).

Hatching success was strongly influenced by MEI_{rainy} over 6 years in leatherback turtles (linear regression: $R^2 = 0.977$, $P < 0.001$) and olive ridley turtles at Playa Grande (linear regression: $R^2 = 0.809$, $P = 0.01$), but not at any other olive ridley site nor at any of the green turtle nesting beaches ($P > 0.05$, all cases) (Fig. 3). Hatching success of all species and at all locations was lowest in 2015–16 (Fig. 4). The effect was strongest in leatherback turtles that led to nearly no production of hatchlings that year (mean \pm SD in 2015–16, $4\% \pm 12\%$), while the effect was very mild in green turtles (just 6% lower than their mean) (Fig. 4). Hatching success of leatherback turtles was by far the lowest in the history of the monitoring project at Playa Grande, which began assessing hatchling production in 2004, and almost no hatchlings were produced coinciding with the extreme El Niño event.

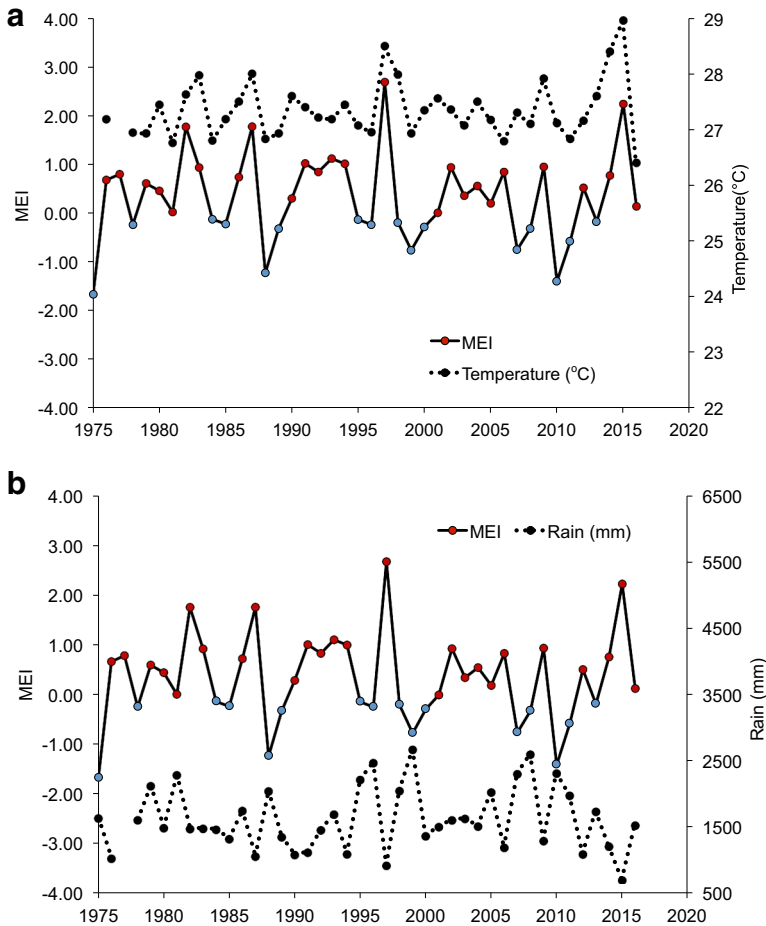


Fig. 1 Average multivariate ENSO index (MEI) and local climatic conditions in North Pacific Costa Rica. Local climatic conditions correspond to **a** local air temperature (°C) and **b** precipitation (mm) registered between 1975 and 2016 during the rainy season (May–November). Red circles indicate El Niño and blue circles La Niña events. MEI values represent averages for the same months of the rainy season

Under the RCP8.5 scenario, climate models projected a four-fold increase in the frequency of extreme events between the end of the nineteenth century and end of twenty-first century (Table 2), from 0.7 events per decade during the second half of the nineteenth century, to 1 event per decade during the second half of twentieth century and to 2.9 events per decade projected by the second half of twenty-first century. This translated into an estimated decline in the mean annual reproductive success over a decade of ~ 19, 1, and 7% in leatherback, green, and olive ridley turtles, respectively (Table 3).

4 Discussion

Climate change has become a growing threat to sea turtle populations as rising temperatures and changes in precipitation patterns can potentially impact foraging dynamics, reduce

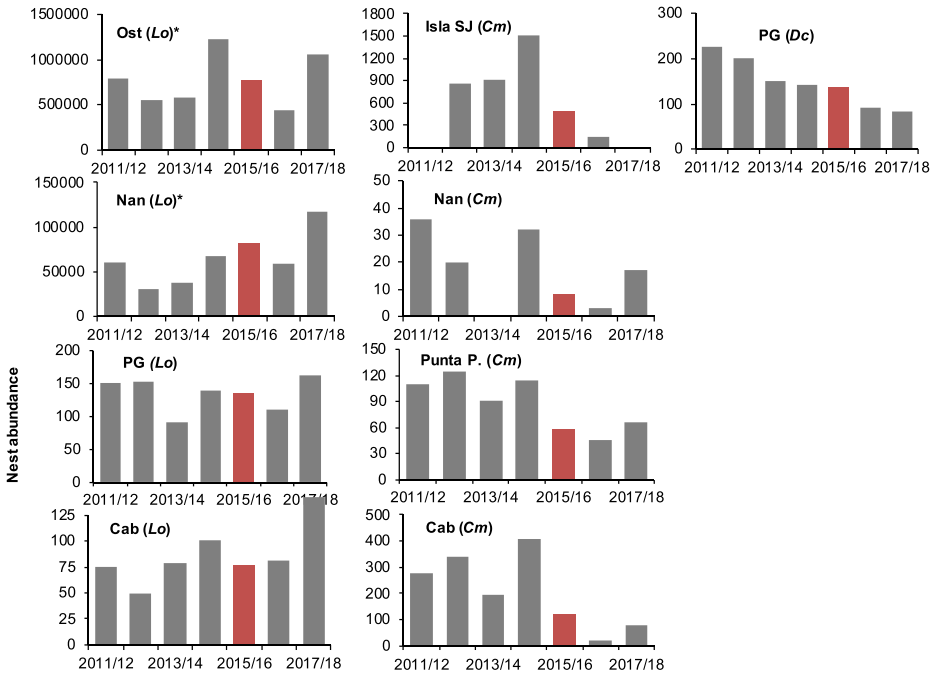


Fig. 2 Nesting abundance of three sea turtle species that nest in North Pacific Costa Rica. Nesting abundance is indicated by number of (1) nests in green turtles (*Cm*) and “*arribada*” olive ridley turtles (*Lo*)* and (2) body pits in leatherback (*Dc*) and solitary olive ridley turtles (*Lo*). Beaches included were (North to South) Isla San José (*Cm*), Nancite (*Cm*, *Lo*), Cabuyal (*Cm*, *Lo*), Playa Grande (*Dc*, *Lo*), Punta Pargos (*Cm*), and Ostional (*Lo*). * indicates *arribada* nesting beaches. No data was available for green turtles at Isla San José and Nancite in 2011 and 2013, respectively. Year of the extreme El Niño event is indicated in red

hatchling output, reproductive frequencies, and/or further bias sex ratios of hatchlings. In some areas along the eastern Pacific coast, such as northern Costa Rica, El Niño events drive changes in local climate towards detrimental conditions for sea turtles. Thus, an increase in the frequency and/or strength of these events could have severe impacts on sea turtles. In the present study, we (1) assessed the impact of extreme El Niño events on three sea turtle species that nest in northwest Costa Rica and (2) projected changes in the frequency of extreme events due to climate change to see how this would affect sea turtle populations.

Hatching success of sea turtle eggs was found to be negatively affected by high temperatures in several sea turtle species and populations (Howard et al. 2014; Montero et al. 2019; Santidrián Tomillo et al. 2009; Valverde et al. 2010). In leatherback turtles, high nest temperature and specially, low precipitation levels increase mortality of eggs and hatchlings in the nest, conditions that are exacerbated during regular El Niño years (Santidrián Tomillo et al. 2012). Local climate in northwest Costa Rica reached extreme conditions in 2015, the hottest and driest year since there were records (Fig. 1). Consequently, the extreme El Niño events had a dramatic effect on the hatching success of leatherback turtles with only 4% of eggs hatching in 2015/16.

Hatching success of leatherback turtles in Costa Rica seems more susceptible to changes in the local climate than in other areas around the world such as the Caribbean and South Africa, possibly due to the generally drier conditions that characterize northwest Costa Rica (Santidrián Tomillo et al. 2015b). Local climatic effects on hatching success have also been

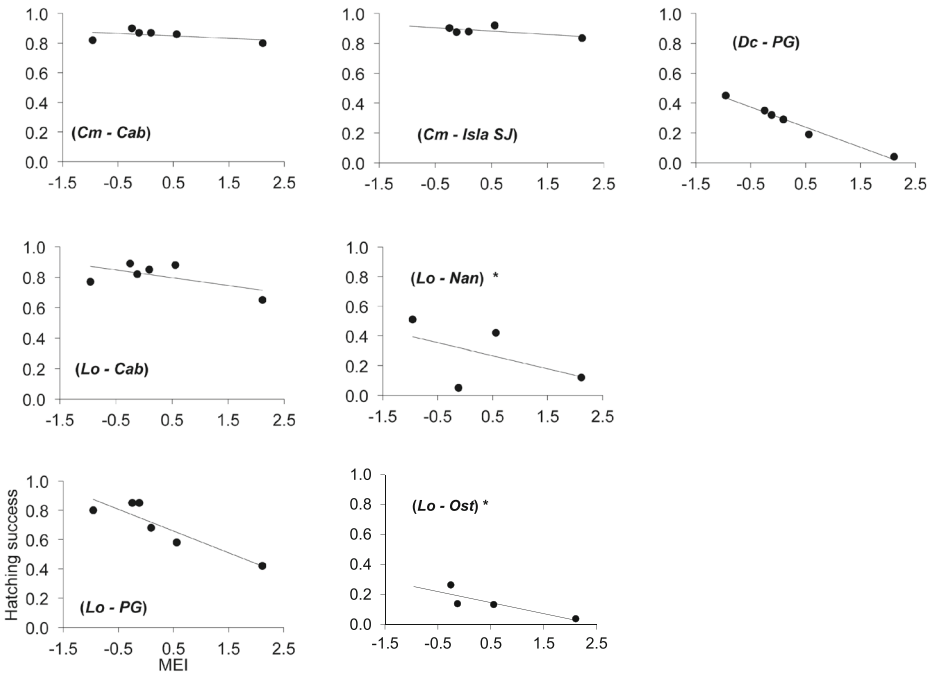


Fig. 3 Annual sea turtle hatching success in Northwest Costa Rica versus the multivariate ENSO index (MEI). Annual hatching success of leatherback (*Dc*), green (*Cm*), and olive ridley (*Lo*) turtle nests between seasons 2011/2012 and 2016/2017 was obtained from Playa Grande (*Lo*, *Dc*), Nancite (*Lo*), and Cabuyal (*Lo*, *Cm*). * indicates arribada nesting beach

reported for loggerhead turtles in Brazil where some differences were found among beaches along the coast (Montero et al. 2019). We also found some differences in the hatching success of olive ridley turtles among beaches in Costa Rica. Nevertheless, decreases were observed at most sites due to the extreme event in both solitary beaches (with still ~ 40 and ~ 65% of eggs hatching) and in Ostional. This suggests that olive ridley turtles, while still vulnerable to changes in climate, are less vulnerable than leatherback turtles. Yet the interpretation of the variability in hatching success in *arribada* beaches is complicated as contamination also reduces hatching success due to the extremely high density of nests (Honarvar et al. 2008). Green turtles on the contrary, appeared largely unaffected by ENSO. Hatching success decreased during the extreme event, but it was still high at ~ 80% at both index beaches for this species (Fig. 4). This indicates a possible resilience of green turtle clutches to climate change, at least in this area, an interesting characteristic that demands further research.

Although extreme events can negatively affect sea turtles, they are long-lived organisms and the impact of an extreme event on their populations could be buffered over long time periods as they reproduce multiple times during their life. This may be the case for green and olive ridley turtles for which, we projected no impacts or very mild long-term effects. However, in leatherback turtles in Pacific Costa Rica, where reproductive success is strongly associated with local climatic conditions, an increase in the frequency of extreme events could lead to a 19% decline in their mean decadal reproductive success. This adds additional pressure to an already reduced nesting population of leatherback turtles, which are critically endangered in the eastern Pacific due to interaction with fisheries, past egg poaching, and climate change (Saba et al. 2012; Santidrián Tomillo et al. 2008, 2017b; Spotila et al. 2000).

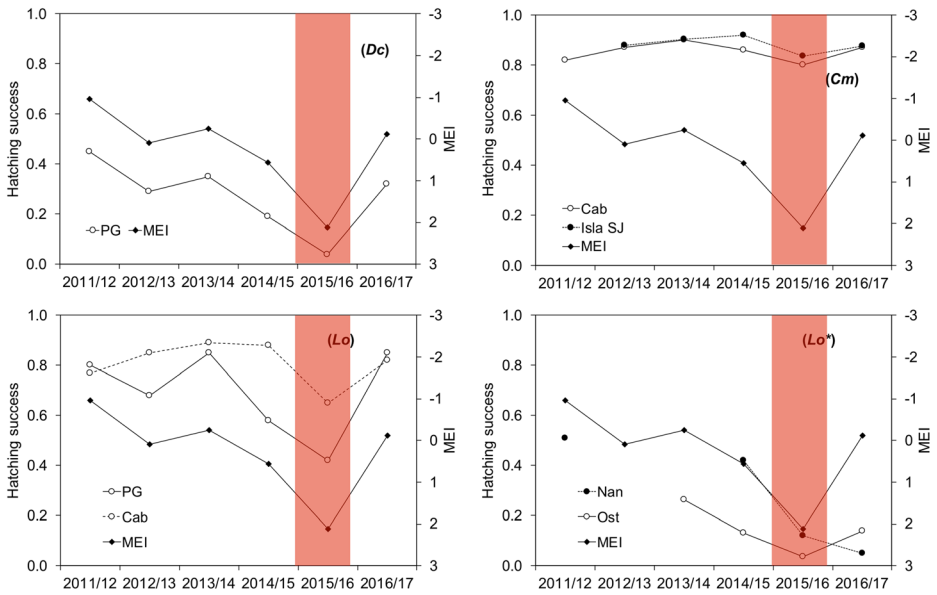


Fig. 4 Changes in annual sea turtle hatching success in Northwest Costa Rica. Annual hatching success of green (*Cm*), olive ridley (*Lo*), and leatherback turtle (*Dc*) nests and the multivariate ENSO index (MEI) between 2011 and 2012 and 2016 and 2017. Beaches included were (North to South) Isla San José (Isla SJ), Nancite (Nan), Cabuyal (Cab), Playa Grande (PG), and Ostional (Ost). The red section indicates the duration of the extreme El Niño event and *indicates the *arribada* nesting beaches. MEI values are in reverse order

Nesting abundance of green turtles was likely affected by the extreme 2015–16 El Niño event. Sea turtles are capital breeders that store energy before migrating and may skip reproduction if foraging conditions are not optimal in a particular year (Saba et al. 2007; Rivalan et al. 2005). Consequently, the number of nesting turtles registered on the beach may be affected by the foraging conditions in the ocean in months or years before the nesting season, as well as by the number of turtles registered in previous seasons (Broderick et al. 2001; Solow et al. 2002). The number of nesting green turtles in northern Australia was related to the ENSO conditions registered 2 years before, with very high numbers occurring after major El Niño

Table 2 Number of extreme events detected by the CMIP5 models. Climate change models included historical (years 1850–2000) and RCP8.5 projections (years 2006–2100). We considered an extreme event when the average austral summer (December–February) rainfall over El Niño 3 was greater than 5 mm per day based on Cai et al. (2014)

Model	Historical			RCP8.5	
	1850–1900	1901–1950	1951–2000	2006–2050	2050–2100
CanESM2	6	6	6	10	17
CESM_CAM5	6	2	9	6	10
CNRM-CM5	1	2	4	4	14
GFDL_CM3	5	3	5	11	14
GISS-E2-H	4	9	5	16	26
MRI_CGCM3	0	0	0	0	6
Mean	3.7	3.7	4.8	7.8	14.5
Mean per decade	0.7	0.7	1	1.7	2.9

events (Limpus and Nicholls 1988). We did not find such an apparent effect of ENSO on the number of green turtles in Costa Rica, with the exception of the 2015/16 El Niño event when nesting abundance was also minimal 1 year after the extreme event. A lack of correlation between MEI and nesting numbers in the whole dataset may be explained by high number of years needed to identify long-term patterns and/or because ENSO conditions occurring in most of the years included in the study were mild (five of the 7 years were on average of neutral conditions; MEI values between -0.5 and 0.5). It is also possible that the relationship between remigration intervals, oceanic conditions, recruitment rates, and nesting numbers are especially complex in the eastern Pacific due to its lower and variable productivity compared with that of other areas. Thus, more years of data and/or more complex modeling may be needed.

Although the low number of nesting leatherback turtles is also explained by a long-term declining trend due to other impacts (Spotila et al. 2000), the effect of ENSO on their reproductive frequency has been previously determined (Saba et al. 2007), which ultimately, may affect the number of turtles registered on the beach. Likewise, the remigration intervals of green turtles could relate to changes in feeding conditions driven by changes in ocean temperature, affecting the number of nesting turtles on the beach as it occurs in the Caribbean and Australia (Limpus and Nicholls 1988; Solow et al. 2002). Variation in remigration intervals is higher in green turtles than in other sea turtle species, which can largely affect the interannual nesting numbers (Broderick et al. 2001). In addition to the effect on the length of the remigration intervals, which has implications for the short and long-term reproductive success of the turtles, food availability could negatively impact the viability of green turtle populations if adult mortality was increased during years of lower productivity. Long-lived sea turtles are more sensitive to changes in adult mortality than in the mortality of early life stages (Heppell et al. 2003). Thus, an effect of extreme events on adult survival could greatly impact their populations. However, at this moment, we cannot assess the relationship between feeding conditions and adult mortality as long-term datasets would be needed.

The different life histories of closely-related species may also explain some of the differences found on the impacts of extreme events. Nesting abundance of olive ridley turtles appeared unaffected by the 2015–16 El Niño. Unlike the other species, olive ridleys follow a slightly different strategy and only lay 1–2 clutches per year and reproduce every year (Dornfeld et al. 2015). This may allow them to lay clutches “as they become ready” in comparison to the other species that need to store enough energy before migrating to lay multiple clutches in a season and survive that time without feeding (Plot et al. 2013). Interestingly, we also found differences

Table 3 Mean estimated annual number of hatchlings produced per female over a decade. The annual number of hatchlings for leatherback, green, and olive ridley turtles was estimated in relation to the frequency of extreme events projected from the CMIP5 models (0.7, 1, and 2.9 events/decade for second half of the nineteenth, twentieth, and twenty-first centuries, respectively). The percentage decline in hatchling production due to extreme events was estimated based on climate change projections over 100 years (second half of the twentieth century to second half of the twenty-first century)

	Annual number of hatchlings per female			% decline due to extreme events
	1851–1900	1951–2000	2051–2100	
Leatherback turtle	121 ± 81	118 ± 78	96 ± 65	18.6%
Green turtle	290 ± 174	289 ± 174	285 ± 171	1.4%
Olive ridley turtle	151 ± 102	150 ± 101	140 ± 94	6.7%

among olive ridley nesting beaches, which suggest that the impacts of ENSO and extreme events may differ and should be assessed at a very local level.

Finally, differences among beaches and species suggest that some populations could bounce back after extreme events, whereas in others, the effects are more long-term and could even be devastating. As aforementioned, the vulnerability of certain populations to extreme events is likely to be exacerbated if their current population levels are already low and they are threatened by other anthropogenic impacts (Spotila et al. 2000) as is the case in critically endangered eastern Pacific leatherback turtles. Thus, extreme events in this species could lead to rapid extinctions given the large impact that these events have on them and the low nesting levels and the impact of other threats. In addition to the global effect of anthropogenic-forced climate warming, sea turtles in areas highly influenced by ENSO are affected by the periodic occurrence of extreme events. Therefore, sea turtles in this region must adapt if they are to survive throughout the twenty-first century, not only to the increasing global mean temperatures (GMTs), but also to an increasing frequency of extreme events that could double even under small levels of warming (Wang et al. 2017). Some climate mitigation strategies could be implemented to counteract the negative effect of high temperature and dryness on the clutches of species affected, such as nest shading or nest irrigation during extreme El Niño events. Because sea turtles have long-generation times, they may not be able to adapt quick enough to the current rate of change. Thus, a proportion of clutches in risk could be relocated to climate-controlled hatcheries where climate mitigation programs could be conducted. Finally, other extreme events such as prolonged precipitation (Rivas et al. 2018), hurricanes, or harmful algal blooms such as red tides could also impact sea turtles, which have not been considered here. Our results highlight the importance of conducting species-specific and site-specific analyses of climate impacts on sea turtles.

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Author contributions PST, LGF, MW, NT and NJR discussed the implications of the extreme 2015–16 El Niño event in Costa Rica and conceived the study. PST, NJR and FVP led and provided data for the projects at Cabuyal and Playa Grande, LGF led and provided data for the projects at Nancite and Isla San José, MW and NT led and provided data for Punta Pargos and CMO led and provided data for Ostional. VSS advised and assisted with the projections of extreme events. PST wrote the manuscript with input from all authors.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interest.

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