Are trends in Olive Ridley sea turtle (*Lepidochelys olivacea*) nesting abundance affected by El Niño Southern Oscillation (ENSO) variability? Sixteen years of monitoring on the Pacific coast of northern Central America

Daniel Ariano-Sánchez [a, b, *], Colum Muccio [c], Frank Rosell [a], Stefanie Reinhardt [a]

[a] Department of Natural Sciences and Environmental Health, Faculty of Technology, Natural Sciences and Maritime Sciences, University of South-Eastern Norway, 3800, Bø, Telemark, Norway
[b] Centro de Estudios Ambientales y Biodiversidad, Universidad Del Valle de Guatemala, 18 Avenida 11-95, Zona 15, 01015, Guatemala
[c] Wildlife Rescue and Conservation Association (ARCAS), Guatemala

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ABSTRACT

Long-term monitoring is essential for the identification of population trends, and to understand how these trends are affected by climate variability. The El Niño Southern Oscillation (ENSO) is the strongest global interannual pattern of climate variability, resulting in the disruption of the annual phenological cycles of sea turtles. Among sea turtles, the Olive Ridley (*Lepidochelys olivacea*) is the most abundant, and on many beaches their nests are relocated to hatcheries as part of conservation management, especially in northern Central America. However, Olive Ridley nesting abundance trends in northern Central America and the effects of ENSO variability on these trends are still not fully understood. Here, we present the first long-term study of this subject. We predicted an upward trend in Olive Ridley nesting abundance on the Pacific coast of Guatemala, and a negative effect of increasing ENSO variability on nesting abundance. As proxies for nesting abundance, we analysed two different data sets; a 16-year period of Olive Ridley nesting data, using nesting tracks from one index beach (Hawaii in Guatemala), and the yearly number of eggs buried in the 25–35 hatcheries that operate along the Pacific coast of Guatemala. Revised Multivariate ENSO Index values were applied to estimate annual ENSO variability. During this 16-year study period, ENSO variability was distributed in eight neutral years, two normal El Niño years, four normal La Niña years and two extreme ENSO events; an extreme La Niña in 2010 and an extreme El Niño in 2015. We found a clear overall upward trend in Olive Ridley numbers of nesting tracks and eggs buried in hatcheries but no clear effect of ENSO variability on these nesting abundance proxies. However, a decrease in the net change of eggs buried in hatcheries occurred the respective years after the two extreme ENSO events during the study period. In the second year after those events, the net change of eggs buried in hatcheries bounced back to resume the overall positive trend. Our results suggest a clear upward trend, resilient to ENSO variability, of the nesting abundance of the Pacific coast Olive Ridley population in Guatemala. Community-based hatchery management efforts seem to be effective for Olive Ridley conservation on the Pacific coast of Guatemala. However, longer term monitoring

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* Corresponding author. Department of Natural Sciences and Environmental Health, Faculty of Technology, Natural Sciences and Maritime Sciences, University of South-Eastern Norway, 3800, Bø, Telemark, Norway.
E-mail addresses: dariano@uvg.edu.gt (D. Ariano-Sánchez), cmuccio@arcasguatemala.org (C. Muccio), Frank.Rosell@usn.no (F. Rosell), stefanie.reinhardt@usn.no (S. Reinhardt).

including additional nesting beaches in northern Central America are necessary to further elucidate the effects of ENSO variability on the nesting abundance of Olive Ridley.

1. Introduction

An increase in climate variability caused by current climate change is greatly affecting biodiversity and annual phenological cycles of many animal species (Cohen et al., 2018). Data series obtained through series of successive observations along several years can reveal long-term trends that may reflect climatic or anthropogenic influences (Sukhotin and Berger, 2013). Long-term monitoring permits the separation of these trends from the noise of highly variable natural data and is especially relevant for the assessment of conservation actions in the context of climatic change (Sukhotin and Berger, 2013; Cheney et al., 2014; Rodríguez-González et al., 2017; Guerra et al., 2019). The El Niño Southern Oscillation (ENSO) is the strongest interannual pattern of climate fluctuation in the world, resulting in global disruption of weather patterns and ecosystem functions (McPhaden et al., 2006; Santoso et al., 2017). Climate change is expected to double the frequency of ENSO events compared to pre-industrial levels, maintaining an increasing trend that will persist long after the stabilization of greenhouse warming (Cai et al., 2014, 2015b; Wang et al., 2017). ENSO involves an irregular alternation between El Niño phases, which consist of increased sea surface temperature and decreased ocean productivity (Cai et al., 2014), and La Niña phases, which show contrary effects (Cai et al., 2015b). Extreme El Niño and La Niña are characterized by even warmer/colder sea surfaces, with Extreme El Niño phase originating in the eastern equatorial Pacific while extreme La Niña phase originates in the central Pacific (McPhaden et al., 2006; Cai et al., 2015a).

Increased climate variability, such as ENSO patterns, might have profound effects on ectothermic organisms such as sea turtles, since environmental cues largely dictate their metabolic rate, sex ratios, migration patterns and affect their phenological cycles (Hawkes et al., 2009; Quiñones et al., 2010; Castro et al., 2012; Patrício et al., 2019; Godley et al., 2020). Sea turtles are known to have clear interannual variability in the number of females nesting at their breeding beaches as females typically do not nest in consecutive years, and spend time feeding at sea between successive nesting years (Broderick et al., 2001; Solow et al., 2002). El Niño events have shown some influence on the interannual variability of the nesting abundance of Leatherbacks (*Dermochelys coriacea*), which is under severe decline in the Pacific, due to egg harvesting and bycatch in fisheries (Saba et al., 2007; Reina et al., 2009; Santidrián-Tomillo et al., 2012, 2020). A recent study carried out over 7 years at six beaches in Costa Rica found no clear correlation between El Niño events and the nesting abundance of Green Turtles (*Chelonia mydas*) and Olive Ridleys (*Lepidochelys olivacea*) but highlighted the relevance of conducting longer term site-specific analyses for these species (Santidrián-Tomillo et al., 2020). However, Green Turtles and Olive Ridleys in the eastern Pacific are showing encouraging populations recoveries in recent years (Ocana et al., 2012; Seminoff et al., 2015; Bézy et al., 2016). The effects of La Niña and overall ENSO variability on the nesting numbers of other sea turtle species has not been studied.

The Olive Ridley is the most abundant sea turtle species in the world (López-Castro et al., 2004; Plotkin et al., 2006; Eguchi et al., 2007; Plotkin, 2010; Dornfeld et al., 2015), and is classified as Vulnerable in the IUCN Red List of Threatened Species (Abreu-Grobois and Plotkin, 2008). In Central America, harvesting of Olive Ridley eggs for local consumption is considered to be one of the species' major threats (Juarez and Muccio 1997; Fonseca et al., 2009; Valverde et al., 2012; Bézy et al., 2016), therefore nest relocation to protected hatcheries is considered an effective conservation management tool for this species (García et al., 2003). The oldest of these hatcheries in Guatemala was established in 1979 and is located at Hawaii beach (Juarez and Muccio, 1997). In recent years, upward trends in sea turtle populations in areas with ongoing long-term sea turtle conservation programs were reported (Ceriani et al., 2019; Godley et al., 2020; Laloë et al., 2020). The identification of proxies of essential variables for long-term monitoring of population trends of endangered species is fundamental for the optimization of conservation efforts in the context of increased climate variability (Guerra et al., 2019). In the case of sea turtles, nesting tracks and number of eggs collected at index beaches are commonly used as effective proxies of their nesting abundance following the Index Nesting Beach Survey (INBS) protocol (SWOT Scientific Advisory Board, 2011).

Herein, we present the first long-term study of Olive Ridley population trends and potential relationships with ENSO variability in northern Central America, using nesting tracks and numbers of eggs buried in hatcheries as proxies of their nesting abundance. Our objectives were to (1) estimate the trend of the nesting abundance of Olive Ridley females, and (2) evaluate the effects of ENSO variability on the nesting abundance of Olive Ridleys on the Pacific coast of Guatemala over a 16-year period (2003–2018). We predicted an upward trend in the abundance estimates of annual nesting females as a result of long-term conservation efforts, such as egg harvest limits, fisheries bycatch mitigation and hatcheries, carried out on the Pacific coast of Guatemala since 1979. Also, we predicted a negative effect of ENSO variability on the nesting abundance of this species.

2. Materials and methods

2.1. Study area

The fieldwork was conducted at Hawaii Beach (13.869012°N, −90.419519°W), a volcanic sand beach located 2 km west of the village of Hawaii, Chiquimulilla, Santa Rosa, on the Pacific coast of Guatemala (Fig. 1a). This beach is located within the Hawaii Protected Area (HPA), a 4000 ha multiple-use zone declared in 2016 that includes one of the largest mangrove wetlands in the country. Five villages are located along the coastline, with small hotels and vacation homes concentrated near the village of Hawaii. Residents of these villages traditionally subsist on fishing, mangrove logging, agriculture and sea turtle egg collection, but tourism is an increasingly important economic activity. The Wildlife Rescue and Conservation Association (ARCAS) administers the HPA from its base at the Hawaii Park, also home to the Hawaii hatchery, the oldest, and historically one of the most productive sea turtle hatcheries on the Pacific coast of Guatemala. Since 1993, ARCAS has operated sea turtle hatcheries in Hawaii and in the village of El Rosario, 6 km to the east, collecting and incubating 40,000−60,000 Olive Ridley eggs per year (Juarez and Muccio, 1997; Brittain et al., 2007). Along with these efforts, ARCAS has carried out standardized nesting track surveys along a 7.5 km transect (Fig. 1b) for monitoring the abundance of annual nesting female Olive Ridleys (Fig. 1c) since 2003.

In-situ incubation of nests is almost non-existent on the Guatemalan Pacific coast, as egg harvesting is an important local economic activity, and local villagers sell the eggs collected to the hatcheries for their re-burial (Fig. 1d). Depending on the resources available, between 25 and 35 other sea turtle hatcheries operate per year along the 254 km Pacific coastline of Guatemala. Under a program sanctioned by the government's National Council of Protected Areas (CONAP), local villagers are permitted to harvest Olive Ridley eggs as long as they give 20% of each nest as a conservation quota, which then is distributed along the active sea turtle hatcheries for re-burial and incubation (Brittain et al., 2007). The central government lacks the resources to implement sea turtle conservation efforts on its own, and a number of private and public sector stakeholders, including non-governmental organizations (NGOs), educational institutions, universities, schools, hotels, and vacation homeowners sponsor sea turtle hatcheries. In theory, only Olive Ridley eggs are allowed for harvesting; all other species are fully protected by law.

2.2. Study species

The Olive Ridley has a circumtropical distribution, occurring in the Atlantic, Pacific, and Indian Oceans (Seminoff et al., 2015). It is one of the smallest of the marine turtles, rarely exceeding 45 kg, with average weights around 35 kg
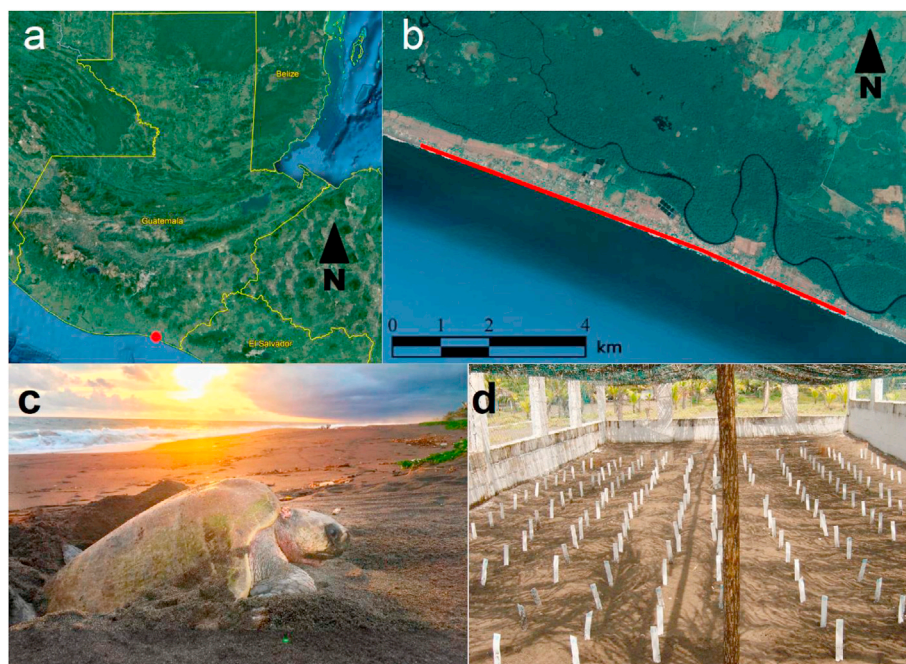

Fig. 1. Study area Hawaii beach (red dot) on the Pacific coast of Guatemala, Central America (a), location of nesting track monitoring transect (red line) at Hawaii beach (b), Olive Ridley (*Lepidochelys olivacea*) nesting at Hawaii beach, in Guatemala (c), and inside view of the Hawaii sea turtle hatchery, where relocated eggs are incubated under protected and controlled conditions (d). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Pritchard, 1979). The mean age at sexual maturity for this species is around 13 years (Zug et al., 2006). Olive Ridleys display two different types of nesting behavior: synchronized mass nesting, known also as arribada, and solitary nesting (Plotkin et al., 2006; Matos et al., 2012). Nesting in Guatemala consists only of solitary nesting that occurs between June and October with peak activity in August and September, although sporadic nesting occurs year around (Juarez and Muccio, 1997).

Olive Ridleys can exhibit strong nesting site fidelity (Matos et al., 2012). They have a maximum of two nesting events per year, every two years with an internesting period ranging from 16 to 25 days (Barrientos-Muñoz et al., 2014). In other parts of Central America, the average clutch size for the species is around 100 eggs per clutch (Da Silva et al., 2007; Valverde et al., 2012), although in Guatemala, clutch size is reported to be 92.7 ± 7.4 eggs (Muccio, 2019).

2.3. El Niño Southern Oscillation variability

We evaluated El Niño Southern Oscillation (ENSO) variability using the Revised Multivariate ENSO Index (MEI.v2) which is a composite of five variables: sea level pressure, sea surface temperatures, 10-m surface zonal wind, 10-m surface meridional wind, and outgoing longwave radiation (Zhang et al., 2019). MEI.v2 captures a more holistic picture of the state of ENSO than do sea surface temperature-based indices (Zhang et al., 2019). We estimated the average of MEI.v2 for the nesting season (July−December) of each year during the study period. ENSO events were considered as extreme when MEI.v2 $> +1.5$ (extreme El Niño) or MEI.v2 < -1.5 (extreme La Niña), normal El Niño when MEI.v2 was between $+0.5$ and $+1.5$, normal La Niña when MEI.v2 was between -1.5 and -0.5, and neutral years when MEI.v2 was between -0.5 and $+0.5$, during the July−December nesting season. The MEI.v2 data were obtained from the Physical Sciences Laboratory (PSL) of the National Oceanic and Atmospheric Administration (NOAA) of the United States of America (PSL, 2020).

2.4. Nesting tracks

Nesting tracks were registered as a proxy for abundance of nesting of Olive Ridley females at the study site, as they are considered an effective estimate for relative abundance of nesting sea turtles especially on beaches with solitary nesting, where the probabilities of confusing nesting tracks from different individuals are low (SWOT Scientific Advisory Board, 2011). The procedure we followed was an adaptation of the Index Nesting Beach Survey (INBS) protocol (SWOT Scientific Advisory Board, 2011). The INBS protocol has proven to be useful for nesting trend assessments and accurate comparisons between years due to fixed start and end dates, fixed time window for daily early-morning surveys, fixed survey boundaries, and specialized standardized training of the different beach surveyors that record the nesting tracks every year (Ceriani et al., 2019). Monitoring the numbers of nesting tracks has the advantages of reduced confusion in the count, and requires less effort needed to perform surveys, but as disadvantage, it doesn't account for variation in nesting success or clutch frequency (SWOT Scientific Advisory Board, 2011).

In our case, the Olive Ridley population-monitoring protocol consists of daily early-morning nesting track count patrols, carried out between July 1st and December 31st (fixed start and end dates, respectively) along the transect (boundaries fixed between 13.879112° N, −90.451536°W and 13.853776° N, −90.385770°W) at Hawaii beach for the period 2003−2018. Trained surveyors hired from local villages identified Olive Ridley nesting tracks according to their shape, flipper pattern and depth, thus confirming nests and distinguishing false crawls. The ending point (body pit) of each nesting track was marked with a GPS location. After marking, the tracks were erased, to prevent repeated counting. Nesting tracks for 2012 were not recorded because of logistical difficulties with the trained staff that year.

The probability of confusion of the species is extremely low because the vast majority (at least 99%) of the sea turtle nests recorded every year for the last 30 years on the Pacific coast have been Olive Ridleys, with infrequent Green Turtle and Leatherback nests (Juarez and Muccio, 1997; Brittain et al., 2007). The only documented nesting of a Hawksbill (*Eretmochelys imbricata*) at the Pacific coast of Guatemala was recorded in 2018 (Muccio and Izquierdo, 2019).

2.5. Number of eggs buried in hatcheries

Number of eggs buried in hatcheries were registered as a complementary proxy of abundance of nesting Olive Ridley females at the study site. Number of eggs harvested or collected are considered an effective estimate to monitor relative abundance of nesting sea turtles as they are a direct measure of their reproductive output (SWOT Scientific Advisory Board, 2011). We used official data of the total number of eggs collected and re-buried in all the sea turtle hatcheries along the 254 km of the Pacific coast of Guatemala, gathered by CONAP. Monitoring the number of eggs buried in hatcheries has the advantage that eggs harvested or collected regularly can be used to monitor relative nesting abundance but has the disadvantage that is difficult to account for variation in clutch size or clutch frequency (SWOT Scientific Advisory Board, 2011). Often, clutches that are laid on one beach are transported, and then buried in hatcheries relatively far from the nesting site. Therefore, it is not possible to make any statement on which part of the coast the eggs actually come from. Eggs from different nests are often combined in the process of collection and transfer, therefore we analysed the total numbers of egg buried in all the operating sea turtle hatcheries for every given year during the 16-year study period, rather than the number of nests, as a proxy for nesting trends on the Pacific coast of Guatemala. In addition, the net change of eggs buried in hatcheries between consecutive years (in percentage) was estimated as a descriptive tool in visualizing annual changes in nesting abundance according to the occurrence of extreme ENSO events. This net change of eggs buried in hatcheries was calculated using the

following formula: (*Total number of eggs buried in hatcheries for the actual year − Total number of eggs buried in hatcheries the year before*)/*Total number of eggs buried in hatcheries the year before* * 100.

2.6. Statistical analysis

We examined the annual trends of nesting tracks and eggs buried in hatcheries with generalized linear models (GLM) with negative binomial distribution to correct for overdispersion (Lindén and Mäntyniemi, 2011), using year and MEI.v2 as fixed effects. Interaction between the fixed effects was included in the list of candidate models to expand the understanding of the relationship among year and MEI.v2 values. The fixed effects used in all analyses were not correlated (Pearson r coefficient < 0.5), and variance inflation factor values were <3 (Zuur et al., 2010). Residuals plots were analysed, showing that homogeneity and normality of residual variance were fulfilled (Zuur et al., 2010).

We developed a list of candidate models based on our hypotheses. Candidate models were analysed with the MASS package (Venables and Ripley, 2002). We carried out model selection based on Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002) to obtain the most parsimonious models and parameter estimates using the MuMIn package (Barton, 2020). When multiple candidate models showed the same level of performance (cumulative Akaike weight > 0.95), we performed model averaging to examine the overall effect size of the predictor variables (Symonds and Moussalli, 2011; Dormann et al., 2018; Harrison et al., 2018). Parameters that included zero within their 95% confidence interval (CI) were considered as uninformative (Arnold, 2010). Mean values are given with standard errors (SE). All analyses were conducted in R 3.6.2 using the RStudio 1.3.959 interface (R Core Team, 2020).

3. Results

We registered 21,775 Olive Ridley nesting tracks at Hawaii beach and 3,740,009 Olive Ridley eggs buried in all hatcheries on the Pacific coast of Guatemala, over the 16-year study period. On average 1520 ± 477 Olive Ridley nesting tracks were registered annually at Hawaii beach, ranging from 906 nesting tracks in 2003 to 2134 in 2017. The mean number of Olive Ridley eggs buried annually in the hatcheries along the Pacific coast of Guatemala was 233,750 ± 172,682, ranging from 46,048 eggs in 2003 to 590,405 in 2018. During this 16-year study period, ENSO variability was distributed in eight neutral years, two normal El Niño years, four normal La Niña years and two extreme ENSO events: La Niña in 2010 and El Niño in 2015 (Table 1).

The models of best fit for predicting the nesting abundance of Olive Ridleys over the study period included year alone or both year and MEI.v2 as fixed effects. Neither MEI.v2 values alone nor the interaction between MEI.v2 values and year were good predictors of nesting abundance in our model selection procedure (Table 2 and Table 3).

3.1. Nesting abundance trends over the 16-year study period

There was a clear upward trend in the number of Olive Ridley nesting tracks and the overall number of eggs buried in hatcheries for the period 2003−2018 (Fig. 2). We found a 236% increase in the number of nesting tracks and a 1282% increase in the number of eggs buried in hatcheries during the same period (Table 1). Nesting tracks showed a wider dispersion of data than the number of eggs buried in hatcheries in our negative binomial fit. According to the effect size of year (Table 3), the

Table 1
Olive Ridley nesting tracks at Hawaii beach, number of Olive Ridley eggs buried in the hatcheries on the Pacific coast of Guatemala, and Revised Multivariate El Niño Southern Oscillation (ENSO) Index (MEI.v2) during the peak nesting season (July−December). Years of extreme ENSO events occurrence are presented in *italics*. Nesting tracks for 2012 were not recorded.

Year	Nesting tracks at Hawaii beach (n)	Total number of eggs buried in all the hatcheries (n)	MEI.v2	MEI.v2 type[a]	Net change in number of eggs buried in hatcheries (%)
2003	906	46,048	0.13	N	−
2004	1,001	60,681	0.48	N	31.78
2005	1,043	85,376	−0.35	N	40.70
2006	1,138	109,839	0.58	EN	28.65
2007	1,280	108,861	−1.03	LN	−0.89
2008	1,370	129,482	−1.03	LN	18.94
2009	1,101	129,526	0.68	EN	0.03
2010	*1,520*	*189,749*	*−2.20*	*ELN*	*46.49*
2011	1,594	172,648	−1.13	LN	−9.01
2012	−	202,310	−0.08	N	17.18
2013	1,237	267,217	−0.40	N	32.08
2014	1,867	311,503	0.18	N	16.57
2015	*2,042*	*394,699*	*1.95*	*EEN*	*26.71*
2016	1,564	352,392	−0.42	N	−10.72
2017	2,134	589,273	−0.70	LN	67.22
2018	1,978	590,405	0.25	N	0.19

[a] N: neutral, EN: El Niño, LN: La Niña, EEN: extreme El Niño, ELN: extreme La Niña.

Table 2

Summary of generalized linear models (GLM) selection for nesting abundance of Olive Ridley sea turtles showing model log-likelihood (LL), Akaike Information Criterion corrected for small sample sizes (AICc), change in AICc (ΔAICc) and AICc weight (wAICc).

Candidate models	LL	AICc	ΔAICc	wAICc
(a) Olive Ridley nesting tracks				
Nesting tracks ~ Year	−91.85	192.1	0.00	0.83
Nesting tracks ~ Year + MEI.v2[a]	−91.77	196.0	3.87	0.12
Nesting tracks ~ Year + MEI.v2 + Year*MEI.v2[a]	−90.17	197.8	5.73	0.05
Nesting tracks ~ MEI.v2	−102.30	213.0	20.89	0.00
(b) Number of Olive Ridley eggs buried in hatcheries				
Number of eggs ~ Year	−159.51	327.4	0.00	0.87
Number of eggs ~ Year + MEI.v2[a]	−159.50	331.4	4.03	0.12
Number of eggs ~ Year + MEI.v2[a] + Year*MEI.v2[a]	−159.36	336.2	8.80	0.01
Number of eggs ~ MEI.v2[a]	−185.56	379.5	52.10	0.00

[a] Revised Multivariate El Niño Southern Oscillation Index.

Table 3

Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of the explanatory variables for the analyses of Olive Ridley nesting (annual nesting tracks at Hawaii beach and annual total number of eggs buried in hatcheries) on the Pacific coast of Guatemala from 2003 to 2018. Informative parameters are given in **bold**.

Variables	Effect size (β)	SE	LCI	UCI
(a) Olive Ridley nesting tracks at Hawaii beach				
Intercept	−92.24	15.86	−123.33	−61.16
Year	**0.05**	**0.01**	**0.03**	**0.06**
MEI.v2[a]	−0.002	0.01	−0.03	0.03
(b) Number of Olive Ridley eggs buried in hatcheries				
Intercept	−295.34	14.56	−323.87	−266.82
Year	**0.15**	**0.01**	**0.14**	**0.17**
MEI.v2[a]	−0.0004	0.01	−0.02	0.02

[a] Revised Multivariate El Niño Southern Oscillation Index.

upward trend was steeper in the number of Olive Ridley eggs buried in hatcheries than in the number of nesting tracks at Hawaii beach.

3.2. ENSO variability effects on nesting abundance

ENSO variability measured with the MEI.v2 values had no effect on the upward trend in Olive Ridley nesting abundance proxies (number of nesting tracks and the number of eggs buried in hatcheries) for the period 2003−2018 (Table 3).

The annual patterns in the net change of eggs buried in hatcheries showed a decrease occurring in the respective first year after the two extreme ENSO events that happened during our study period (Fig. 3). The year after the extreme La Niña event of 2010 showed a decrease of 9.01% (2011) and the year after the extreme El Niño event of 2015 showed a decrease of 10.71% (2016) in the total number of eggs buried in hatcheries between consecutive years. Despite these two yearly decreases, the net change of eggs buried in hatcheries increased again in the second year after those extreme ENSO events, resuming the overall upward trend in the numbers of eggs buried.

4. Discussion

Our findings provide evidence of an increasing trend in the nesting abundance of Olive Ridley sea turtles on the Pacific coast of Guatemala during the 16-year study period. There was no clear effect of ENSO variability measured with the MEI.v2 index on Olive Ridley nesting tracks. A more detailed exploration of the annual net change of eggs buried in hatcheries according to the ENSO type of each year showed a decrease occurring in the respective first year after the extreme ENSO events during our study period. However, the net change of eggs buried in hatcheries bounced back to positive values two years after these extreme events.

4.1. Nesting abundance trends over the 16-year study period

The upward trend in the nesting abundance of Olive Ridleys on the Pacific coast of Guatemala is consistent with the recovery of other populations of sea turtle species, as for example, at several disjunct Green Turtle nesting beaches all around the world with long-term, community-based conservation programs (Troëng and Rankin, 2005; Seminoff et al., 2015; Silva et al., 2017; Patrício et al., 2019). In recent years, more examples of modest upward trends in population numbers have
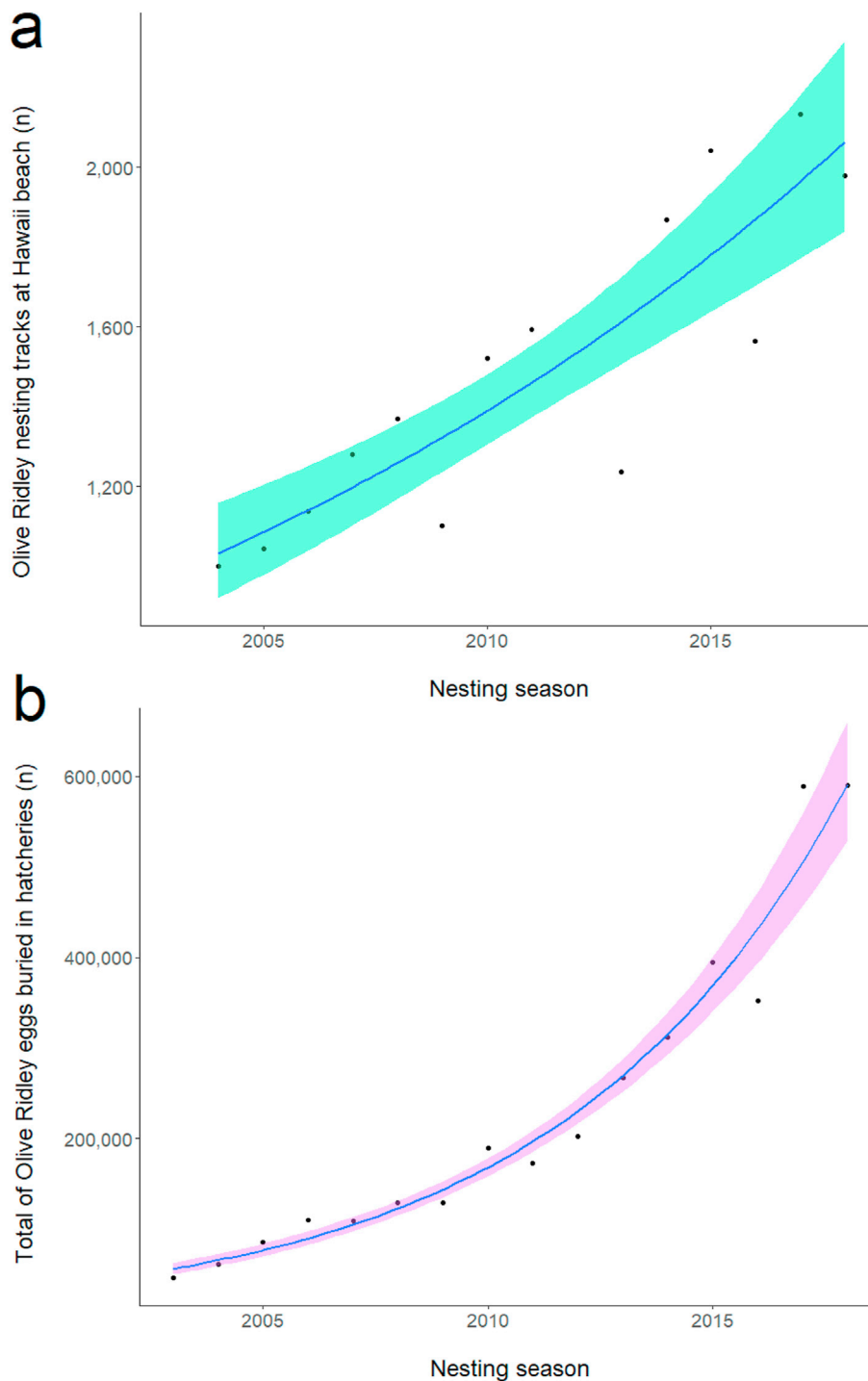
Fig. 2. Annual trends in Olive Ridley nesting tracks at Hawaii beach (a) and number of eggs buried in hatcheries along the Pacific coast of Guatemala (b) during the period 2003–2018. Predicted values by the most parsimonious models are shown in solid blue line with 95% confidence intervals shaded in color. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

also been reported, among many others, for Hawksbills at American Samoa and Marianas islands in the western Pacific (Becker et al., 2019) and Loggerheads (*Caretta caretta*) at Cape Verde archipelago in western Africa (Laloë et al., 2020). These upward trends in sea turtle populations at the local level are believed to be a result of long-term conservation programs that involve beach protection, mitigation of fisheries bycatch and the use of hatcheries for nest translocation (García et al., 2003;
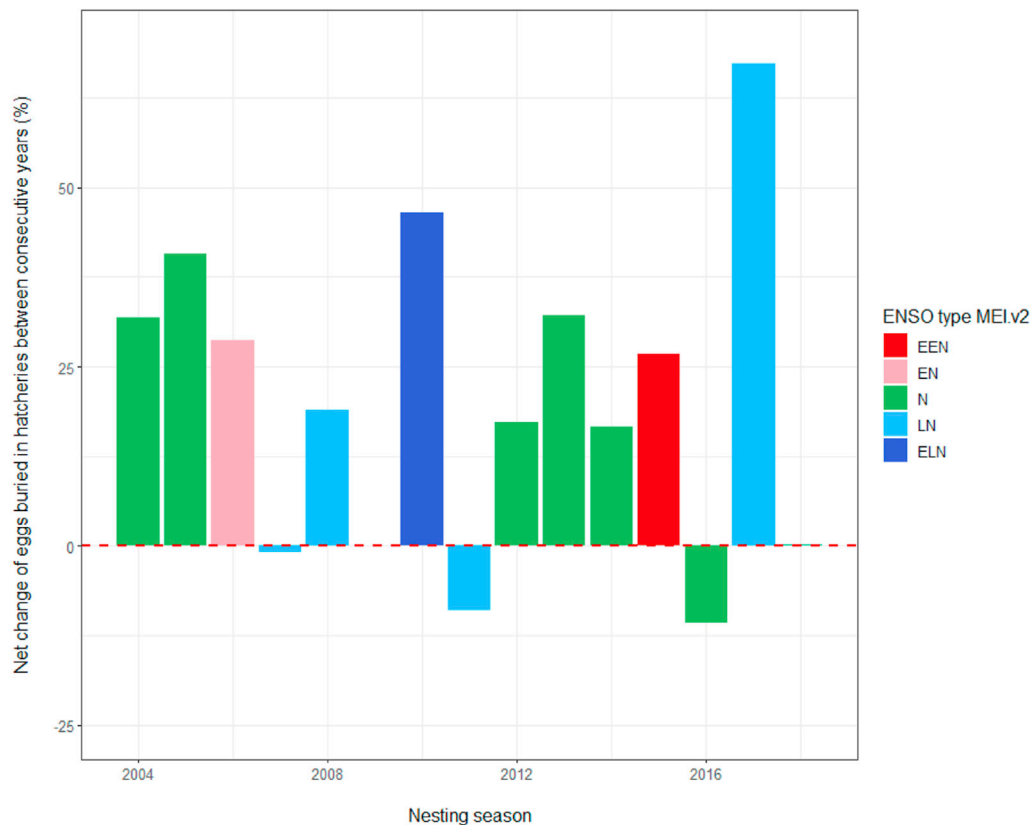
Fig. 3. Annual net change in percentage of Olive Ridley eggs buried in hatcheries between consecutive years along the Pacific coast of Guatemala reported for the period 2003−2018. Bars are colored according to El Niño Southern Oscillation (ENSO) phase type based on the Revised Multivariate ENSO Index (MEI.v2). EEN: extreme El Niño (MEI.v2 < −1.5), EN: El Niño (+0.5 < MEI.v2 < +1.5), N: neutral years (−0.5 < MEI.v2 < +0.5), LN: La Niña (−1.5 < MEI.v2 < −0.5), ELN: extreme La Niña (MEI.v2 < −1.5) in the corresponding nesting season year.

Ceriani et al., 2019; Godley et al., 2020). However, among sea turtles, Leatherbacks have shown dramatic declines presumably due to overharvesting of eggs, fisheries interactions in the open ocean and climate change (Saba et al., 2007; Reina et al., 2009; Santidrián-Tomillo et al., 2012).

Of the extant sea turtle species, the Olive Ridley is one of the species that have shown more robust population recovery in recent years (Eguchi et al., 2007; Peavey et al., 2017) after extremely low numbers in the past century (Fonseca et al., 2009). A very notable recovery documented for Olive Ridleys has occurred at Escobilla beach, in Oaxaca Mexico, which in the 1980s was almost decimated and has since recuperated to become one of the largest arribada sites in the world (Hernández-Echeagaray et al., 2012; Ocana et al., 2012). Other sites with notable Olive Ridley recoveries are Ostional, in Costa Rica (Valverde et al., 2012; Bézy et al., 2016), La Flor, in Nicaragua (Honarvar et al., 2016), Sergpipe, in Brazil (Da Silva et al., 2007) and Gahirmatha, in India (Behera et al., 2010).

Our findings show that the nesting population of Olive Ridleys at the Hawaii beach in Guatemala might also be recovering, after over-harvesting of eggs caused extremely low nesting numbers that were first documented in the late 1990s (Juarez and Muccio, 1997). Taking into account that Olive Ridleys reach sexual maturity at an age of approximately 13 years (Zug et al., 2006), we consider our 16-year study period as representative to detect nesting population trends at the site. *In-situ* nest incubation of Olive Ridleys has almost been non-existent in Guatemala during the last decades, which suggests the positive nesting trends are likely the result of almost 30 years of intensive, participatory, hatchery-based conservation efforts. Long-term conservation efforts that include beach protection and nest relocation to hatcheries have also contributed to reversing nesting declines of endangered sea turtle populations such as Green Turtles at Tortuguero, Costa Rica (Troëng and Rankin, 2005) and Olive Ridleys at Playa Cuixmala, México (García et al., 2003). However, our results need to be interpreted with caution as they represent only a fraction of the Olive Ridley population, the nesting females, at the Pacific coast of Guatemala, and conservation actions, such as the 20% conservation quota for egg collectors, must be maintained on site.

4.2. ENSO variability effects on nesting abundance

The absence of clear ENSO effect measured with the Multivariate ENSO Index (MEI) on the nesting abundance of Olive Ridleys is consistent with the findings of a 7-year period study (2011−2018) carried out in Costa Rica (Santidrián-Tomillo et al.,

2020). These authors consider that the lack of correlation between MEI and the nesting numbers of Green Turtles and Olive Ridleys in their study may be explained by too few study years to identify long-term patterns and the prevalence of average neutral ENSO conditions (only two non-neutral ENSO years). In our 16-year study period, we encompass eight non-neutral ENSO years, but still face limitations since the ENSO variability was distributed in eight neutral years, two El Niño years, four La Niña years and only two extreme ENSO events: La Niña in 2010 and El Niño in 2015. However, the absence of clear ENSO effects on the nesting abundance of Olive Ridleys may also be explained by the species' trophic position as benthic carnivores. They feed on crabs, shrimps, bivalves, and benthonic fishes, which are generally present in some form during all years, allowing them to switch prey items to maximize energy intake and thus maintain nesting output (Wildermann and Barrios-Garrido, 2012; Colman et al., 2014; Poggio et al., 2014). Benthic carnivorous sea turtle species such as Loggerheads are known to present less interannual variability than herbivorous species such as Green Turtles (Broderick et al., 2001).

Our results showed a decrease in the annual net change of Olive Ridley eggs buried in hatcheries in the first year following an extreme ENSO event, but no decrease in the net change of nesting track numbers. Unfortunately we were unable to determine if these reductions are consistent over time due to the small number of extreme ENSO events (extreme La Niña of 2010 and extreme El Niño of 2015) during the study period. The decrease in the annual net change of eggs buried in hatcheries without a clear reduction of nesting tracks the year after the extreme ENSO events can be a product of a decrease in the number of eggs per clutch laid by females, while the numbers of nesting females at the site remain the same. A similar decrease in the reproductive output was found in Green Turtles during and after extreme ENSO events (Santidrián-Tomillo et al., 2020). Reduced marine food abundance is a common effect of extreme ENSO events (Chavez et al., 2011), and this could prevent sea turtles from accumulating sufficient body fat for the breeding season of the following year, leading to a reduction in reproductive output and average number of eggs per clutch (Bjorndal et al., 2017). Alternatively, the impact of extreme ENSO events on Olive Ridley populations may not be significant given the multiple breeding events during their long lifetime (Santidrián-Tomillo et al., 2020), their relatively short time for reaching sexual maturity (Zug et al., 2006), and their migratory flexibility to adapt to their large dynamic marine ecosystem (Plotkin, 2010; Peavey et al., 2017). Additionally, Olive Ridley populations that are subject to hatchling production in managed hatcheries may be more resilient to the long-term effects of ENSO variability on nesting trends, as these hatcheries artificially control nest temperatures and protect against nest predation.

The identification of proxies of essential variables for long-term monitoring is useful for the optimization of available operational resources (Guerra et al., 2019). We suggest a continuing long-term monitoring of both proxies of Olive Ridley nesting abundance (number of eggs buried in hatcheries and nesting tracks) as both are complementary and can provide a clearer picture of the nesting population trend and its relationship to extreme ENSO events at the study site. On the one hand, the number of eggs buried in hatcheries has a lower dispersion of data during the study period and are a more direct measurement of the reproductive output than nesting track counts. On the other hand, nesting tracks are independent of the capacity of the hatcheries to purchase eggs in addition to the 20% conservation quota, although they are subject to the abilities of local patrollers to accurately detect nesting tracks. In the end, community-based monitoring of nesting beaches is often considered as the only feasible and low-cost approach for assessing sea turtle populations in developing countries (Olendo et al., 2019).

4.3. Relevance of community-based conservation efforts of sea turtle hatcheries

Although sea turtle conservation has taken a largely non-consumptive approach over the last decades, there is a clear need to adapt conservation strategies to include sustainable use by local communities (Valverde et al., 2012; Godley et al., 2020). In recent years, sea turtle hatcheries on the Pacific coast of Guatemala have incorporated local egg collectors in their management and have also benefitted from increased support from hotels and vacation home owners for the purchase of eggs for the hatcheries. Since 2017, most sea turtle egg collectors have preferred to sell the remnant 80% of the eggs they collect to hatcheries, instead of selling them for human consumption, knowing that the eggs sold to hatcheries are contributing to the conservation of the species. This has evolved into a win-win relationship between local egg collectors and sea turtle hatcheries. Locals receive economic benefits from their egg collection work, and sea turtle hatcheries receive increased numbers of eggs for *ex-situ* incubation, raising the number of Olive Ridley hatchlings released every year. This increased capacity of hatcheries to buy eggs in addition to the 20% conservation quota may explain the steeper increase in the number of eggs buried in hatcheries particularly shown in the last three years, compared to the increase in the number of nesting tracks over the same period.

In developing countries, the empowerment of local communities has shown to be fundamental for success in natural resources management, especially when conservation actions contribute to create local livelihoods (Barrientos-Muñoz et al., 2014; Nilsson et al., 2016; Olendo et al., 2019). Olive Ridley eggs make a significant contribution to the local economies of the villages at the Pacific coast of Guatemala. Thus, we recommend the continuation of the 20% conservation quota along with the strengthening of the win-win relationship between sea turtle hatcheries and local eggs collectors.

Further studies are required to determine if the current hatchling production in the hatcheries along the Pacific coast of Guatemala is sufficient to maintain a stable Olive Ridley population. Age-specific mortality rates, sex ratios, shoreline habitat destruction and numbers of pelagic adults are still unknown factors for this population. However, strengthening the community-based conservation efforts at Guatemalan sea turtle hatcheries seems fundamental to ensuring the resilience of Olive Ridleys to ENSO variability and other aspects of climate change.

5. Conclusions

Our results suggest a clear increase in nesting abundance of the Olive Ridley sea turtle population along the Pacific coast of Guatemala over our 16-year study period. This upward trend in nesting abundance was resilient to ENSO variability. Given only two extreme events occurred during the time frame of our study, continued long term monitoring will better elucidate the possible effects of extreme ENSO events on the nesting abundance of Olive Ridleys. Nonetheless, community-based hatchery management efforts seem to be essential for this population to cope with increased ENSO variability.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01339.

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