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El Niño events and chlorophyll levels affect the reproductive frequency but not the seasonal reproductive output of East Pacific green turtles

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ABSTRACT: The El Niño-Southern Oscillation (ENSO), which includes El Niño and La Niña phases, affects oceanographic conditions and primary productivity of marine ecosystems at a global scale. During El Niño events, warm temperatures in the central and eastern tropical Pacific decrease primary productivity, affecting the biology of many species including sea turtles. We aimed to determine the effect of ENSO (as a global index) and primary productivity in the foraging areas (as a local index) on remigration intervals (number of years between nesting seasons) and seasonal reproductive output (clutch size and number of clutches in a season) of green turtles *Chelonia mydas* in the North Pacific off Costa Rica, an area highly influenced by ENSO. We used the Multivariate ENSO Index (MEI) and mean values of chlorophyll *a* from previously identified feeding areas for this population over different time periods (up to 3 yr before the nesting season). Chlorophyll *a* levels in foraging areas and MEI strongly influenced the reproductive frequency of green turtles. Variability in the remigration intervals was better explained by models that included chlorophyll levels 2 and 3 yr before the onset of the nesting season and MEI conditions in the previous 3 yr. Models using global and local indexes were equally good at predicting changes in the remigration intervals. Positive values of MEI (El Niño phase) and lower levels of chlorophyll *a* corresponded to longer remigration intervals. No statistically significant relationships were found between seasonal reproductive output and MEI or chlorophyll *a* levels. As El Niño events may become more frequent and last longer due to climate change, the lifetime reproductive output of green turtles in this area may be compromised in the future.

KEY WORDS: El Niño-Southern Oscillation · ENSO · Breeding frequency · Productivity · Foraging grounds · Marine ecology · Sea turtle · *Chelonia mydas* · Costa Rica

1. INTRODUCTION

Oceanographic and atmospheric conditions, such as surface temperature or sea level, fluctuate on seasonal and inter-decadal scales (Tourre et al. 2005). The most significant climate variability on the inter-annual time scale is that of the El Niño-Southern Oscillation (ENSO). ENSO is a climatic phenomenon composed of 2 distinct phases, El Niño and La Niña. In the eastern Pacific, the winds in the equatorial zone during the El Niño phase are weaker and there is a deeper thermocline, which causes hot water to rise to the surface (Ji & Leetmaa 1997). Consequently, primary productivity in these areas decreases, affecting the productivity of the ocean. Conversely, in periods of La Niña, temperatures are colder and this results in increased productivity, especially in the equatorial Pacific, where La Niña originates (Behrenfeld et al. 2001).

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The El Niño events of 1982–1983, 1997–1998 and 2015–2016 were the strongest on record (Gergis & Fowler 2009, Huang et al. 2016, Zhai et al. 2016), and produced a significant reduction in primary productivity in the equatorial Pacific, falling by as much as 5 to 10 times in 1982–1983 (Barber & Chavez 1983, Strutton & Chavez 2000). As a result, various groups along the food chain were affected, such as macroalgae species that disappeared from the intertidal zone (Vinueza et al. 2006); corals that suffered from bleaching (Reyes-Bonilla et al. 2002, Brainard et al. 2018); fisheries (e.g. jack mackerel in Chile and anchovy in Peru) (Sánchez et al. 2000, Arcos et al. 2001); sea lions that showed decreased reproductive success (Sielfeld & Guzmán 2002); and fin whales, for which a reduction in density was observed (Benson et al. 2002).

El Niño events also affect sea turtles at multiple levels. For example, they may decrease the growth rate and size of maturation in female green turtles *Chelonia mydas* at the Galapagos Islands, possibly due to low nutrient intake (Carrión-Cortez et al. 2010). Annual variability in the number of clutches and nesting females of green turtles in the Indo-Pacific (Limpus & Nicholls 2000, Chaloupka 2001) and leatherback turtles *Dermochelys coriacea* in the eastern Pacific (Saba et al. 2007) is also influenced by ENSO. In addition, El Niño events also decrease hatching success and hatchling emergence in leatherback (Santidrián Tomillo et al. 2012) and olive ridley turtles *Lepidochelys olivacea* (Valverde et al. 2010) in Costa Rica.

Reproductive investment in sea turtles is high. Sea turtles lay 50 to 130 eggs in a clutch, but green, loggerhead *Caretta caretta* and hawksbill turtles *Eretmochelys imbricata* can lay as many as 190 eggs per clutch (Limpus 2009). They also lay multiple clutches during a season, nesting as many as 10 (green turtles) (Limpus et al. 2001), 7 (loggerhead turtles) (Tucker et al. 2018) and 14 (leatherback turtles) (Eckert et al. 2012) times per season. Tracking turtles with telemetry and GPS units has also shown that clutch frequencies could be much higher than those estimated based on mark-recapture data (Esteban et al. 2017), especially when nest-site fidelity is low. As sea turtles are capital breeders and most likely have aphagia while nesting (Hamann et al. 2002, but see Tucker & Read 2001), they must accumulate sufficient energy reserves prior to migration to the nesting area (Hamann et al. 2002, Plot et al. 2013) to fuel egg production and the cost of migration. Consequently, turtles do not lay eggs every year and several years elapse before they reproduce again. Since reproductive frequency of sea turtles depends on their ability to store energy, variability in ocean productivity can affect their remigration intervals.

The green turtle is considered one of the great herbivores of the oceans, feeding in tropical and temperate coastal waters (Limpus & Nicholls 2000). Many green turtles feed on macroalgae while others forage seagrass and mangrove fruits (Bjorndal 1997, Limpus 2009, Shimada et al. 2014). Occasionally, they can consume macroplankton like jellyfish as well as small crustacea (Limpus 2009, Shimada et al. 2014). As they are mostly primary consumers, intake and capacity to build up reserves prior to the nesting season can be severely affected by variations in primary productivity caused by ENSO. In Atlantic green turtles, remigration intervals are usually 2 or 3 yr (Troëng & Chaloupka 2007). The remigration intervals of sea turtles in areas influenced by ENSO, such as leatherback turtles in the eastern Pacific (Saba et al. 2007, 2008, Reina et al. 2009) and green turtles in the Caribbean (Solow et al. 2002), can be affected by changes in sea surface temperature due to their effect on primary productivity. The objective of this study was to determine how ENSO and primary productivity in foraging areas affect reproductive frequency and seasonal reproductive output of green turtles that nest in Northwest Costa Rica, an area highly influenced by ENSO. We also compare the use of global or local indexes to assess the effect of climatic conditions on sea turtles.

2. MATERIALS AND METHODS

We conducted night beach patrols between September and March over 9 nesting seasons (from 2010–2011 to 2018–2019) at Cabuyal (10° 40′ N, 85° 39′ W), Northwest Costa Rica. Nesting turtles were tagged with a PIT (Passive Integrated Transponder) tag and a metal tag (INCONEL) on their right front flipper, which allowed identification of the turtles in subsequent encounters (Santidrián Tomillo et al. 2015). We also conducted morning surveys to verify nesting activities and to record nesting events that could have been missed. Beach coverage (number of turtles identified/number of nesting attempts) at Cabuyal is high (over 80 %) and the probability of missing a turtle in the nesting season is very low, because they nest, on average, 4.3 times (Valverde-Cantillo et al. 2019).

2.1. Remigration interval and seasonal reproductive output

We calculated remigration intervals as the time in years that it took 1 turtle to nest again, so only turtles identified in >1 season were included. We used estimated clutch frequency (number of clutches in a season) and clutch size (average number of eggs per clutch) as measures of seasonal reproductive output. The observed internesting period was defined as the number of days between confirmed clutches within a season. The estimated clutch frequency was calculated by dividing the number of days elapsed between the first and last nest for each turtle by the mean observed internesting period for all turtles, and adding 1 to account for the first nest (Reina et al. 2002). We only included values of estimated clutch frequency >1, corresponding to turtles that nested at least twice in Cabuyal in the same season. Since some turtles tagged at Cabuyal have occasionally been seen nesting on other beaches, selecting turtles that were seen twice or more reduced the probability of including turtles that exhibit low nest-site fidelity. To estimate the mean number of eggs per clutch and per turtle, we included turtles for which we counted eggs more than once (this included 80.9% of the females seen in a season).

2.2. El Niño-Southern Oscillation

We obtained information on ENSO from the National Oceanic and Atmospheric Administration (NOAA) of the USA (available at www.esrl.noaa.gov/psd/enso/mei, accessed April 25, 2019). The Multivariate ENSO Index (MEI) is a global index that combines atmospheric and oceanic variables (sea level pressure, sea surface temperature, zonal and southern surface wind and long wave radiation) and simplifies ENSO assessment into a single index. Positive MEI values over 0.5 correspond to El Niño events and negative ones below −0.5 are associated with La Niña.

We used a total of 6 variables to analyze the effect of MEI (Table 1). Since there are no baseline studies on the effect of ENSO on green turtles in the eastern Pacific, but it is known that turtles accumulate reserves over long time periods, and that the number of nesting turtles may be affected 1 or 2 yr after environmental changes occur (Limpus & Nicholls 1988, 2000, Chaloupka 2001), we considered mean values of MEI over different time periods (1 to 3 yr) and up to 3 yr before the onset of the nesting season (Table 1). Years were considered from September of one year to August of the next.

2.3. Primary productivity in foraging areas

The main foraging area identified for green turtles that nest on the Pacific coast of Costa Rica was located between southern Mexico and the Gulf of Papagayo, Costa Rica (between 10° 20′ 47.82″ and 14° 59′ 25.20″ N, over 1000 km of coast and to the 200 m depth isoline) (Blanco et al. 2012, Clyde-Brockway 2014). Levels of chlorophyll *a* (chl *a*; an indicator of primary productivity) in this area were correlated with the abundance of nesting events recorded at Cabuyal (Valverde-Cantillo et al. 2019). We used these chlorophyll levels as a local index, as they are very specific to this population. To quantify the levels of chl *a* in this area, data from the Aqua MODIS satellite were obtained with a spatial resolution of 4 × 4 km (NOAA, available at https://coastwatch.pfeg.noaa.gov/, accessed May 22, 2019). The data were presented as daily chl *a* values from which monthly and annual averages were calculated (in mg m^{-3}). We used annual values from 2007 to 2018. As with the MEI values, mean chl *a* values were calculated for different time periods. For each nesting sea-

Table 1. Summary of variables used in the analysis in relation to each nesting season. We calculated mean values of Multivariate ENSO Index (MEI) and chl *a* over different time periods (1 to 3 yr) starting in September of 1, 2 or 3 years before the onset of the nesting season (-1, -2 or -3, respectively). We specify the period of time included in each variable and use season 2012–2013 as an example (green turtle nesting season extends from September of one year to March of the next)

Variable	Time period included	In relation to nesting season 2012–2013
MEI -1/chl *a* -1	1 yr (Sep to Aug, 1 yr before)	From Sep 2011 to Aug 2012
MEI -2/chl *a* -2	1 yr (Sep to Aug, 2 yr before)	From Sep 2010 to Aug 2011
MEI -3/chl *a* -3	1 yr (Sep to Aug, 3 yr before)	From Sep 2009 to Aug 2010
MEI -1,-2/chl *a* -1,-2	2 yr (mean of -1 and -2)	From Sep 2010 to Aug 2012
MEI -2,-3/chl *a* -2,-3	2 yr (mean of -2 and -3)	From Sep 2009 to Aug 2011
MEI -1,-2,-3/chl *a* -1,-2,-3	3 yr (mean of -1, -2 and -3)	From Sep 2009 to Aug 2012

son, chl *a* levels were calculated for 6 different variables (Table 1). In addition, the level of chl *a* recorded in the month of February prior to the nesting season (chl *a* February) was used as a variable, since the number of nesting turtles at Cabuyal has previously been found to be correlated with chl *a* levels during this time (Valverde-Cantillo et al. 2019).

2.4. Statistical analyses

All statistical analyses were performed with R software (version 3.5.2) and all graphs were represented using the package ggplot2 (Wickham 2016) and mgcViz (Fasiolo et al. 2020). We used the Shapiro-Wilk test to assess the normality of the data (Shapiro & Wilk 1965), the Breusch-Pagan test (Breusch & Pagan 1979) for homoscedasticity and the RESET test for linearity (Ramsey 1969). Both linear models (LM) and generalized linear models (GLMs, with negative binomial distribution; link = 'logit') were used to model the effect of MEI and chl *a* on estimated clutch frequency and clutch size. GLMs were only used when 1 of the assumptions (normality, homoscedasticity or linearity) were not met. These models were verified with visual data exploration. Similarly, LMs were used to find out if 1 of the 3 responses variables (remigration interval, number of eggs and estimated clutch frequency) were affected by any of the others, i.e. if there were trade-offs between variables. In addition, a Pearson's correlation test was performed between MEI and levels of chl *a* to assess the relationship between these variables.

We used generalized additive models (GAMs) to examine the non-linear effect of MEI and chl *a* variables on remigration intervals. The gam function of the mgcv package (Wood 2017) available for R was applied using the Poisson family for each variable with a value of $k = 6$. Overdispersion of data was checked with the DHARMa package (Hartig 2018). Finally, all GAMs were compared using the corrected Akaike's information criterion (AIC_c) value, obtained with the AICcmodavg package in R (Mazerolle 2019). Although there are different recommendations for the cutting criteria for a 'top model set', we used the top 2-AIC_c to select the best models (Burnham & Anderson 2001).

3. RESULTS

We tagged 280 green turtles between 2010–2011 and 2018–2019. Of these, 73 nested in >1 season. Mean (±SD) remigration interval for the nesting population was 3.6 (±0.9) yr. The season with the highest number of turtles was 2014–2015, with a total of 93 turtles identified, and the season with the lowest activity was 2016–2017 with 8 turtles, which took place after an extreme El Niño event (Table 2).

3.1. Effect of ENSO and primary productivity on seasonal reproductive output

We found a statistically significant negative correlation between MEI and ch*l a* levels in foraging areas ($r = -0.62$, $p = 0.03$; Fig. 1). In years of El Niño events (high MEI values), chl *a* values were lower, and vice versa (Fig. 2).

No statistically significant relationships were found between remigration intervals and number of eggs ($p = 0.821$) or between remigration intervals and estimated clutch frequency ($p = 0.186$), indicating that there were no trade-offs between the time elapsed

Table 2. Number of nesting green turtles identified per season at Cabuyal, number and percentage of turtles that nested in a season and returned to the beach to nest in later years, number and percentage of turtles that nested in a season and never returned to the beach, mean estimated clutch frequency (ECF), mean clutch size (for all clutches encountered) and mean remigration interval (RI) (number of years elapsed since turtles were previously seen) for all turtles that nested in a season

Season	Total number of turtles	Turtles returned		Turtles not returned		Mean ECF	Mean clutch size	Mean RI (yr)
		No.	%	No.	%			
2011–2012	73	28	38.4	45	61.6	5.2	70.0	
2012–2013	76	20	26.3	56	73.7	6.2	67.6	
2013–2014	41	6	14.6	35	85.4	6.4	73.0	3.0
2014–2015	93	1	1.1	92	98.9	5.6	67.9	3.2
2015–2016	25	3	12.0	22	88.0	5.8	67.4	3.2
2016–2017	8	1	12.5	7	87.5	7.1	67.0	3.0
2017–2018	20	0	0.0	20	100.0	6.4	60.8	5.0
2018–2019	41	0	0.0	41	100.0	4.2	70.0	4.5

between breeding seasons and the seasonal reproductive output. Likewise, we found no statistically significant relationships between MEI or chl *a* levels and clutch size ($p > 0.05$ in all cases; see Table A1 in the Appendix). There were no statistically significant relationships between MEI or chl *a* and estimated clutch frequency ($p > 0.05$), except between chl *a* -1,-2 and estimated clutch frequency, although the R^2 in this case was very low ($R^2 = 0.04$, $p = 0.033$; see Table A2).

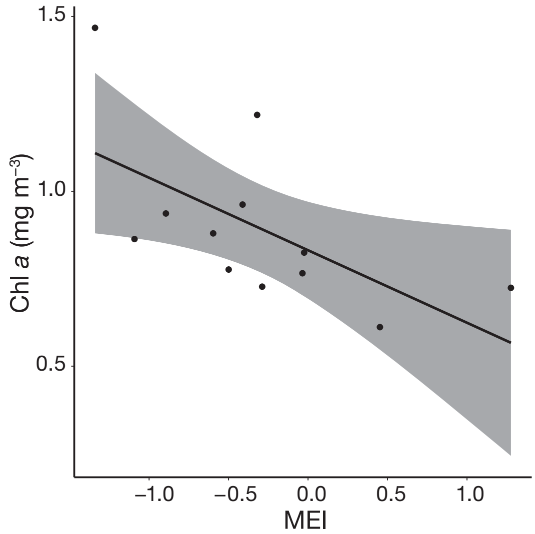

Fig. 1. Relationship between the annual Multivariate ENSO Index (MEI) and the annual chl *a* levels of the foraging areas (expressed in mg m^{-3}) for the green turtle population that nests at Cabuyal (Pearson's correlation: $r = -0.62$, $p = 0.03$). Grey area represents 95 % confidence interval

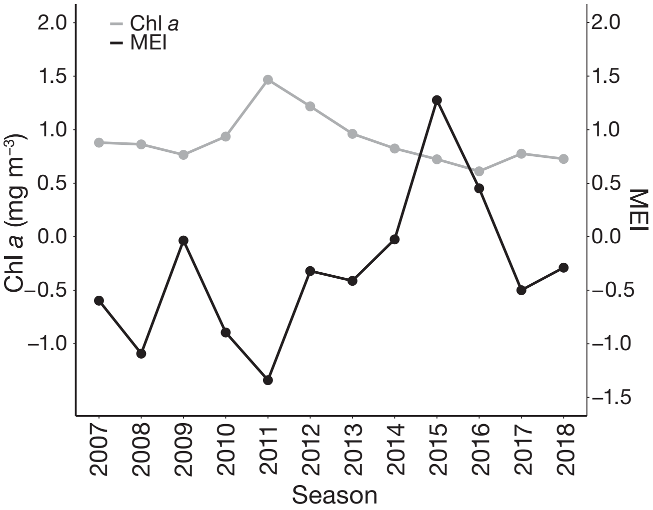

Fig. 2. Changes in chl *a* levels (annual mean) at the foraging areas of the green turtles that nest at Cabuyal and the Multivariate ENSO Index (MEI) between 2007 and 2018

3.2. Effect of ENSO and primary productivity on the remigration interval

GAMs showed a statistically significant relationship between the remigration intervals and all predictor variables, except for MEI -2 and MEI -1,-2 (Table 3). The best model (lowest AIC$_c$ value) showed a positive relationship between the remigration intervals and MEI -3 (deviance explained by the model = 44.1 %, $p = 0.001$), indicating that at higher MEI values (El Niño events), the remigration interval of the turtles was longer (Table 3, Fig. 3).

Table 3. Summary of the GAM models that relate remigration intervals to the different predictor variables. The p-value, the percentage of deviation explained by the model and the value of AIC$_c$ (corrected Akaike's information criterion) are specified for each model. The dashed line marks the models with an AIC$_c$ that differs by less than 2 points from the first model

Predictor variable	p	% deviation	AIC$_c$
MEI -3	0.001	44.1	265.807
Chl *a* -2,-3	0.003	45.8	266.335
Chl *a* -1,-2,-3	0.004	43.3	266.934
MEI -2,-3	0.001	36.9	267.543
Chl *a* -3	0.006	41.8	268.324
Chl *a* -2	0.010	38.9	269.075
Chl *a* -1,-2	0.012	35.4	269.406
MEI -1	0.026	33.5	270.512
Chl *a* -1	0.035	36.3	270.929
MEI -1,-2,-3	0.018	20.6	271.905
Chl *a* February	0.044	15.2	273.363
MEI -2	0.121	8.5	275.182
MEI -1,-2	0.899	0.1	277.436

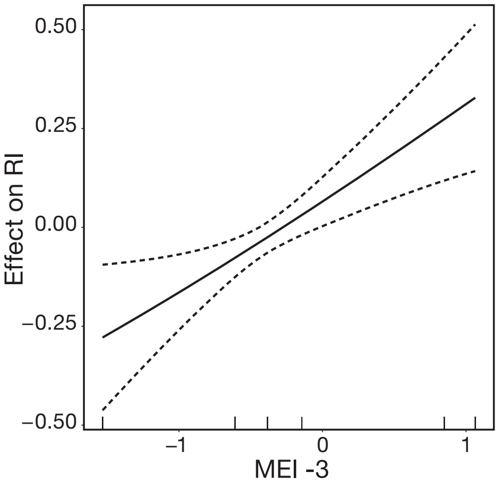

Fig. 3. Effect of the mean annual Multivariate ENSO Index (MEI) 3 yr before the nesting season (MEI -3) on the remigration interval (RI). The smooth curve is the result of fitting a generalized additive model with splines. The broken lines represent twice the standard error on the local estimates at each point

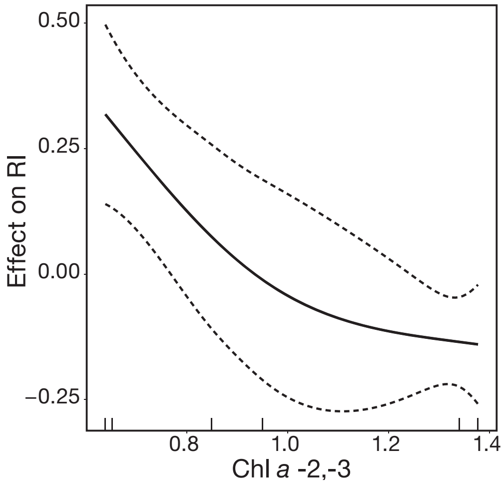

Fig. 4. Effect of chl *a* 2 and 3 yr before the nesting season (chl *a* -2,-3) on the remigration interval (RI). The smooth curve is the result of fitting a generalized additive model with splines. The broken lines represent twice the standard error on the local estimates at each point

The model with the second lowest AIC_c was the one that related chl *a* -2,-3 with the remigration intervals (explained deviance = 45.8%, p = 0.003). In this case, the higher the chl *a*, and consequently the primary productivity, the shorter the remigration interval (Fig. 4). In addition, models chl *a* -1, -2, -3 and MEI -2,-3 were good predictors, as they had AIC_c values that did not exceed the best model by 2 points (Table 3). All models showed the same relationship. As chl *a* increased, the remigration interval decreased, and as the MEI increased, the remigration interval became longer.

4. DISCUSSION

Green turtle remigration intervals were affected by the oceanic conditions in the Pacific Ocean, and this relationship was detected using a global index (MEI) or a local one (levels of chl *a* in the feeding areas). This shows that the remigration intervals of green turtles nesting in Cabuyal depend on both global and local changes due to the existing high correlation between these variables (Fig. 1), as local productivity is driven by ENSO in the Pacific Ocean (Boyce et al. 2010).

Variability in oceanic conditions also impacts other groups such as birds (Bost et al. 2009, Monticelli et al. 2014, Van Dort 2018), mollusks (Angeles-Gonzalez et al. 2017), fish (Potts et al. 2014) and marine mammals (Biuw et al. 2007, Bost et al. 2009, Nachtsheim et al. 2019), with varying effects on abundance, reproduction or behavior. Likewise, a relationship between oceanographic conditions and nesting parameters has previously been found in other sea turtle populations, being characterized by a time lag between the change in oceanic conditions and a change in nesting numbers. For example, ENSO conditions in the foraging areas in the pre-nesting season determined the probability of nesting for leatherback turtles, with this probability being lower at higher MEI values (Saba et al. 2007, 2008). Chaloupka et al. (2008) also detected an inverse correlation between nesting abundance of loggerhead turtles *Caretta caretta* and mean annual sea surface temperature in the feeding areas during the year prior to the nesting season. Other populations of green turtles, such as those nesting in Australia, equally experience large fluctuations in the number of nesting females 2 yr after the occurrence of environmental changes (Limpus & Nicholls 2000). Our results are also in accordance with those of Bruno et al. (2020), who reported fewer green turtle clutches 2 yr after El Niño events.

In eastern Pacific green turtles, low oceanic productivity, indicated by high MEI values and low chl *a* values, resulted in longer migration intervals. The variability in the remigration intervals that we found in green turtles was better explained by the mean oceanic conditions registered 2 and 3 yr before the onset of the nesting season (especially for MEI variables, the best models were MEI -3 and MEI -2,-3). In the case of chl *a*, the best models were chl *a* -2,-3 and chl *a* -1,-2,-3, the latter including the conditions in the previous year. The fact that chlorophyll levels in the year before influenced the variability in the remigration intervals, but MEI values in the previous year did not, suggests that there may be a time lag time between changes in oceanic conditions (ENSO in our case) and local productivity (Meinen & McPhaden 2000, Zhang et al. 2019).

The slightly longer time lag found in our studied population (up to 3 yr) compared to that described for other populations, could be explained by the foraging diet of green turtles. Green turtles are mainly herbivorous and therefore their food has a lower amount of protein (Seminoff et al. 2002), which could explain why it takes longer to obtain sufficient reserves to nest. Follicle development in sea turtles may be postponed to the following year, under adverse feeding conditions, if turtles do not reach a sufficient threshold of reserves for vitellogenesis (Solow et al. 2002). In addition, it seems that the effects of El Niño events on chl *a* levels may last several years. Vinueza et al. (2006) observed changes in algae composition in the Galapagos Islands during and 3 to 5 yr after the 1997−1998 El Niño event. Likewise, Barber et al. (1996) detected changes in primary productivity in the equatorial Pacific during and after the 1991−1992 El Niño event. This effect of El Niño events on primary productivity may help explain why the number of turtles at Cabuyal has remained low over several nesting seasons after the strong El Niño event that took place in 2015.

We used the AIC_c value to determine which models better explained the remigration intervals of green turtles (those with lowest AIC_c values, Table 3). We used a cut-off threshold of 2-AIC_c based on the work of Burnham & Anderson (2001). Using a 6-AIC_c cut-off is sometimes preferred, being less stringent; however, both options allow complex models to be retained (Richards 2008). Although there is some discussion on the suitability of using AIC_c for model selection (Burnham et al. 2011), we think that it correctly identified the best models. Models with low AIC_c were good predictors of remigration intervals, as also indicated by the high level of deviance explained and the highly significant p-values (Table 3).

The seasonal reproductive output of the green turtles that nest at Cabuyal appears to be unaffected by either ENSO or primary productivity at the foraging areas. This is similar to observations reported for the leatherback turtle population that nests at Playa Grande, Costa Rica, in which seasonal reproductive output was not affected by ENSO either during the transition period from the extreme El Niño of 1997−1998 to the La Niña of the following year (Reina et al. 2009). As discussed in Section 1, sea turtles are capital breeders and they obtain energy reserves for reproduction and for migration to the nesting area in advance (Hamann et al. 2002). Therefore, if they do not accumulate sufficient resources to survive reproduction and migration, they do not migrate (Solow et al. 2002) and wait until conditions are adequate. This may explain why we found no effect of oceanographic conditions on the seasonal reproductive output. Sea turtles seem to have an 'all or nothing' reproduction, making a full reproductive investment if they decide to migrate or waiting to the following year if they cannot afford it.

More frequent occurrences of El Niño have been registered in recent decades (Trenberth & Hoar 1997, Allan 2000, Fedorov & Philander 2000). Climate change projections also show an increase in the amplitude of El Niño, related to the strength of the seasonal cycle (Guilyardi 2006) and a greater frequency of occurrence of extreme El Niño events (Timmermann et al. 1999, Cai et al. 2014). If El Niño events become longer, occur more often or become more extreme, this could lead to increased remigration intervals, with fewer nesting turtles. This could decrease the lifetime reproductive output of the individual turtles, and that of the whole population. Projections focused on the occurrence of extreme events of El Niño showed a decline in the reproductive success of leatherback and olive ridley turtles, but not in that of green turtles (Santidrián Tomillo et al. 2020). However, the study did not consider the effect of El Niño events on reproductive frequency. Factoring the effect of El Niño on remigration intervals could infer different results. The effect of climate change on green turtles could seem milder than that on other species because their clutches are more tolerant to high temperatures (Santidrián Tomillo et al. 2020). However, interannual variability in nesting numbers is higher in green turtles than in other species, probably because they feed at the base of the food chain (Broderick et al. 2001). The viability of their populations could decrease under climate change scenarios if the reproductive frequency is reduced due to poor feeding conditions, especially taking into consideration that there are other direct anthropogenic threats, such as illegal egg harvesting or mortality due to interaction with fisheries. Our work contributes to the understanding of the effect of ENSO on green turtles nesting on the Pacific coast of Costa Rica. An increase in the frequency, length and/or strength of El Niño events, as projected by climate change models, could severely compromise green turtle populations in areas highly influenced by ENSO.

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Appendix. Summary of models that tested the effect of the predictor variables on clutch size and estimated clutch frequency

Table A1. Summary of the models used to test the effect of the Multivariate ENSO Index (MEI) and chl *a* on the clutch size of green turtles. The R^2, p-value and type of model used are specified (LM: linear model, GLM: generalized linear model)

Predictor variable	R^2	p	Normality	Homoscedasticity	Linearity	Type of model
MEI -1	<0.001	0.87	Yes	Yes	Yes	LM
MEI -2	<0.001	0.48	Yes	Yes	Yes	LM
MEI -3	0.02	0.09	Yes	Yes	Yes	LM
MEI -1,-2	<0.001	0.56	Yes	Yes	Yes	LM
MEI -2,-3	0.02	0.11	Yes	Yes	Yes	LM
MEI -1,-2,-3	0.009	0.15	Yes	Yes	Yes	LM
Chl *a* -1	<0.001	0.38	No	Yes	Yes	GLM
Chl *a* -2	0.001	0.28	Yes	Yes	Yes	LM
Chl *a* -3	<0.001	0.98	No	Yes	Yes	GLM
Chl *a* -1,-2	<0.001	0.69	Yes	Yes	Yes	LM
Chl *a* -2,-3	<0.001	0.20	No	Yes	Yes	GLM
Chl *a* -1,-2,-3	0.001	0.51	No	Yes	Yes	GLM
Chl *a* February	<0.001	0.06	No	Yes	Yes	GLM

Table A2. Summary of the models used to test the effect of the Multivariate ENSO Index (MEI) and chl *a* on the estimated clutch frequency of green turtles at Cabuyal. The R^2, p-value and the type of model used are specified (LM: linear model, GLM: generalized linear model). *Model statistically significant

Predictor variable	R^2	p	Normality	Homoscedasticity	Linearity	Type of model
MEI -1	0.003	0.24	Yes	Yes	Yes	LM
MEI -2	<0.001	0.62	Yes	Yes	Yes	LM
MEI -3	<0.001	0.24	Yes	No	Yes	GLM
MEI -1,-2	<0.001	0.58	Yes	Yes	Yes	LM
MEI -2,-3	0.009	0.16	Yes	Yes	Yes	LM
MEI -1,-2,-3	<0.001	0.62	Yes	Yes	Yes	LM
Chl *a* -1	0.004	0.22	Yes	Yes	Yes	LM
Chl *a* -2	<0.001	0.15	Yes	No	Yes	GLM
Chl *a* -3	<0.001	0.83	Yes	Yes	Yes	LM
Chl *a* -1,-2*	0.04	0.03	Yes	Yes	Yes	LM
Chl *a* -2,-3	0.006	0.20	Yes	Yes	Yes	LM
Chl *a* -1,-2,-3	0.02	0.08	Yes	Yes	Yes	LM
Chl *a* February	0.13	0.72	Yes	No	Yes	GLM

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