

Multidecadal trends in the nesting phenology of Pacific and Atlantic leatherback turtles are associated with population demography

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ABSTRACT: Knowledge of the mechanisms influencing phenology can provide insights into the adaptability of species to climate change. Here, we investigated the factors influencing multi-decadal trends in the nesting phenology of the leatherback turtle *Dermochelys coriacea* at Playa Grande, Costa Rica, in the eastern Pacific Ocean and at Sandy Point, US Virgin Islands, in the western Atlantic Ocean. Between 1993 and 2013, the median nesting date (MND) at Playa Grande occurred later, at a rate of ~ 0.3 d yr⁻¹. In contrast, between 1982 and 2010, the MND at Sandy Point occurred earlier, at a rate of ~ 0.17 d yr⁻¹. The opposing trends in the MND of each population were not explained by variation in the multivariate El Niño-Southern Oscillation index, North Atlantic Oscillation index, or Atlantic Multidecadal Oscillation index; however, the MND at Playa Grande was significantly correlated with nesting population size. We propose that changes in demography, linked to the population decline at Playa Grande, and the population recovery at Sandy Point may explain the contrasting trends in MNDs. If the observed trends in MND continue into the future, the nesting season at Playa Grande will coincide with increasingly adverse conditions for hatching success, exacerbating the already detrimental effects of climate change. Alternatively, shifts in the nesting phenology may make the Atlantic populations more resilient to climate change. Our findings highlight the increasing need for conservation efforts for eastern Pacific leatherback turtles to consider climate change mitigation practices.

KEY WORDS: *Dermochelys coriacea* · Nesting season · ENSO · NAO · MEI · Population size

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INTRODUCTION

As global temperatures continue to rise, there is increasing concern over the ability of organisms to adapt to these changes (Hoffmann & Sgrò 2011, Doney et al. 2012, Pike 2014). A potential plastic response to climate change is a shift in the timing of

seasonal biological phenomena, termed phenology (Parmesan 2006). By migrating and reproducing when seasonal weather patterns are cooler, many migratory species have mitigated some of the detrimental effects of a warming climate on reproductive success (Møller et al. 2008). Yet such adaptive trends are not universal among species (Both et al. 2009) or

even populations (Gordo 2007). Understanding why different populations express divergent responses to climate change requires an understanding of the factors governing the phenology of a species (Gienapp et al. 2007). Moreover, such knowledge is necessary for developing bioclimatic envelope models with the capacity to accurately predict the response of a species to climate change at regional, or even global, scales (Guisan & Thuiller 2005).

Sea turtles nest on tropical and sub-tropical beaches during distinct nesting seasons that generally last between 3 and 6 mo. The timing of the nesting season must, at least partially, coincide with seasonal temperature and precipitation patterns that create suitable conditions for incubating eggs on the beach (Pike 2013). As climate change progresses, however, shifts in phenology may be required to maintain the nesting season within optimal beach conditions. Indeed, a recent climate-forced population model for the eastern Pacific leatherback turtle *Dermodochelys coriacea* predicted that the anticipated reduction in hatching success resulting from a warming climate could be partially offset if the nesting season shifts to earlier in the year when conditions are cooler and wetter (Saba et al. 2012). Incubation temperatures also govern the gender of the developing hatchlings, with females being produced at higher temperatures (Binckley et al. 1998). Shifts in nesting phenology could therefore have the additional benefit of counteracting female-biases in hatchling production (Doody et al. 2006). However, no previous studies have investigated whether leatherback turtles are likely to respond to climate change through adaptive shifts in nesting phenology.

The factors governing nesting phenology have only been investigated for only 2 sea turtle species: loggerhead turtles *Caretta caretta* (Weishampel et al. 2004, Pike et al. 2006, Mazaris et al. 2013) and green turtles *Chelonia mydas* (Pike 2009, Weishampel et al. 2010, Dalleau et al. 2012). For both species, it has been repeatedly shown that the timing of the nesting season is influenced by the sea surface temperature of the waters near the nesting grounds (e.g. Weishampel et al. 2004, 2010, Mazaris et al. 2008, Dalleau et al. 2012). However, leatherback turtles are uniquely able among sea turtles to maintain elevated and constant body temperatures through a series of adaptations termed gigantothermy (Paladino et al. 1990, Southwood et al. 2005, Bostrom & Jones 2007). The effect of temperature on the nesting phenology of leatherback turtles may therefore be less distinct. Consequently, determining the factors influencing leatherback nesting phenology likely requires the in-

vestigation of a broader range of oceanographic variables. Furthermore, even though local climate conditions directly affect hatching success (Santidrián Tomillo et al. 2009, 2012), environmental conditions at the nesting beach are unlikely to govern when a turtle will arrive at the nesting beach, although they may do so over long time scales through natural selection (Berteaux et al. 2004). This is because leatherback turtles conduct extensive reproductive migrations, and the distance between nesting grounds and foraging areas can extend across entire ocean basins (Benson et al. 2011, Witt et al. 2011). As a result, the nesting grounds are often physically disconnected from the climate of the foraging area.

Leatherback turtles forage exclusively on gelatinous zooplankton, a polyphyletic taxon whose distribution is strongly tied to physical oceanographic conditions (Graham et al. 2001). As a result, the broad-scale distribution and abundance of gelatinous zooplankton are often tied to large oceanographic phenomena, such as the El Niño-Southern Oscillation (ENSO; Raskoff 2001), North Atlantic Oscillation (NAO; Lynam et al. 2004), and the Atlantic Multidecadal Oscillation (AMO; Edwards et al. 2013). Such oceanographic phenomena are therefore also linked to foraging success in leatherback turtles (Saba et al. 2007, Reina et al. 2009). Moreover, the relationships observed between oceanographic conditions and the onset of migration towards the nesting grounds has led to the hypothesis that turtles foraging in more productive areas are able to acquire resources more rapidly, allowing them to migrate to their nesting grounds earlier (Saba et al. 2007, Sherrill-Mix et al. 2008). In addition, as leatherback turtles are expected to forage while migrating (Lambardi et al. 2008), a decrease in food availability en route could result in increased time spent searching for food and a longer migration duration. Better foraging conditions could even increase the number of clutches that each female lays in the upcoming nesting season. This would extend the length of time that each turtle spends at the nesting grounds and may even extend the length of the nesting season.

Beyond the impacts of foraging success, nesting phenology may also be related to factors such as population size or structure (Votier et al. 2009, Shirai 2013). Larger populations of Dalmatian pelicans *Pelecanus crispus* and great white pelicans *Pelecanus onocrotalus* nest earlier than smaller populations (Doxa et al. 2012). In many birds, older individuals also tend to nest earlier in the year than younger individuals (Hipfner et al. 2010). Similar trends have been observed in leatherback turtles, as older and/or

more experienced individuals tend to arrive earlier to nest and lay more clutches (Santidrián Tomillo et al. 2009, Rafferty et al. 2011). As a result, populations with an older mean age may have both earlier and longer lasting nesting seasons (Ezard et al. 2007).

In the present study, we investigated the nesting phenology of 2 leatherback turtle populations over multiple decades. Firstly, we determined whether there had been a change in the timing or length of the nesting season over the study period. Secondly, we investigated whether interannual patterns in nesting phenology were influenced by oceanographic conditions experienced prior to departing the foraging area, while departing the foraging area, during migration, or after arriving at the nesting grounds. Thirdly, we investigated whether nesting phenology was affected by population size. Lastly, to discern how any shifts in nesting phenology may be influencing the conditions experienced by the developing nests, we compared historic trends in nesting phenology to local air temperatures and precipitation levels.

We obtained nesting data from 2 of the longest tagging programs for nesting leatherback turtles: Playa Grande, Costa Rica (10° 20' N, 85° 51' W), in the eastern Pacific Ocean and Sandy Point, US Virgin Islands (17° 40' N, 64° 52' W), in the western Atlantic Ocean. We chose these 2 sites because both support long-term (≥ 20 yr) tagging programs, are located in separate ocean basins, and have experienced contrasting population trends in recent years, with the population decreasing at Playa Grande (Santidrián Tomillo et al. 2007, F. V. Paladino unpubl. data) and increasing at Sandy Point (Dutton et al. 2005, USFWS unpubl. data). By investigating 2 distinct populations, we aimed to investigate differences in the capacity of leatherback turtles from either the Pacific or Atlantic Ocean to respond to climate change via adaptive shifts in nesting phenology.

MATERIALS AND METHODS

Study sites

Playa Grande is a sandy beach, 3.6 km long, on the Pacific coast of Costa Rica. Playa Grande is part of a 3-beach complex, along with nearby Playa Ventanas (1 km long) and Playa Langosta (1.3 km), all of which are used by substantial numbers of nesting leatherback turtles (Reina et al. 2002). Together, these beaches host an estimated 70% of the entire leatherback population nesting on the eastern Pacific shores of Costa Rica and have the highest density of nesting

leatherback turtles in the eastern Pacific Ocean. Of these 3 beaches, Playa Grande has supported the longest running monitoring program for leatherback turtles (since 1993/94) and has the majority of the nesting activity (70 to 90%; Reina et al. 2002). In the present study, we thus exclusively used data collected on Playa Grande.

Sandy Point is a dynamic sandy beach (3.0 km long) on the coast of St. Croix, US Virgin Islands, in the Atlantic Ocean. A tagging program for nesting leatherback turtles at Sandy Point has been in place since 1978. Even though consistent saturation tagging (the concept of identifying every nesting turtle on a specified beach) has only been achieved since 1982, this still remains one of the longest running saturation tagging programs for leatherback turtles worldwide.

Nesting dates

At both locations, the nesting season began in the coolest month of the year and lasted for approximately 6 mo; at Playa Grande, the nesting season was between October and March, while at Sandy Point it was between March and August. Over the nesting season, the beaches were patrolled nightly to encounter nesting females as well as to count and identify tracks of missed turtles. In this manner, a track was recorded for every sea turtle emergence even if the turtle itself was not encountered.

For logistical reasons, the start and end dates of the monitoring programs differed between years. We accounted for this sampling bias by cropping the available datasets to include only the longest consistently patrolled sampling period for all of the years in the study. For Playa Grande, this was between 1 November and 10 February (a total of 132 d) from 1994/95 until 2011/12, and for Sandy Point, this was between 1 April and 5 July (95 d) from 1982 until 2010.

Differences in the monitoring methodologies between Playa Grande and Sandy Point affected our ability to calculate nightly nesting activity. At Playa Grande, observers recorded whether or not a track contained a body-pit, i.e. a large disturbance in the sand that is formed during the initial stages of the nesting process. At Playa Grande, around 10% of the turtles were missed and only a body-pit was seen. Although it is difficult to confirm whether a leatherback turtle nested from visual inspection of only its tracks, body-pits were readily identifiable from the tracks, and 90% of body pits were shown to result in a nest (Reina et al. 2002). Consequently, we used

body-pit counts as our measure of nesting activity at Playa Grande. At Sandy Point, it was not the practice to record from a track whether a body-pit was made or not. Therefore, we used confirmed nest counts (where the turtle was witnessed laying) as our measure of nesting activity at Sandy Point. At this location, less than 5% of turtles were missed each year.

Using the daily body-pit counts at Playa Grande and daily nest counts at Sandy Point, we calculated the median nesting date (MND). We added 1 d to the median nesting dates during each leap year. We also calculated the standard deviation of the mean nesting date. We termed this measure the central tendency of the nesting season (CT_{ns}). As sea turtle nesting seasons can be roughly fit to a normal distribution (Girondot et al. 2007), the CT_{ns} could be used as a proxy for the length of the nesting season.

Ocean conditions

We compared the MND and CT_{ns} to the multivariate ENSO index (MEI) for turtles nesting at Playa Grande, and to the NAO and AMO indices for turtles nesting at Sandy Point. These oceanographic indices provide a univariate representation of oceanographic conditions within the Pacific or Atlantic Oceans. Values for the MEI, NAO, and AMO were accessed from www.esrl.noaa.gov/psd/enso/mei/, www.cpc.ncep.noaa.gov/products/precip/CWlink/pna/nao_index.html, and www.esrl.noaa.gov/psd/data/correlation/amon.us.data, respectively.

To determine whether oceanographic conditions influence the MND and CT_{ns} , we chose to average the MEI or NAO over discrete periods of time that would best coincide with different parts of the migratory cycle. To this extent, we averaged the MEI and NAO over 4 discrete 3 mo periods that encompassed the year preceding the month of peak nesting, which was December for Playa Grande and May for Sandy Point. From earliest to latest, the 3 mo periods represented the conditions (1) before departure from the foraging areas, (2) during departure from the foraging areas, (3) during migration from foraging to nesting grounds, and (4) upon arrival at the nesting grounds. These 3 mo time periods were chosen because post-nesting leatherback turtles require between 2 and 6 mo to reach their foraging areas (James et al. 2005, Shillinger et al. 2008) and leatherback turtles generally only nest every 2 to 7 years (Reina et al. 2002). Thus we assumed that the pre-nesting migrations would take a similar length of time and remain in their foraging grounds for many

months before returning to their nesting areas. Furthermore, the nesting seasons at Playa Grande and Sandy Point last around 6 mo, with the majority of turtles arriving in the first 3 mo.

Population size

At Playa Grande and Sandy Point, passive integrated transponder (PIT) tags with unique ID numbers were implanted into every turtle encountered over the nesting season. As leatherback turtles nest an average of 7 times per nesting season (Reina et al. 2002) and there was a ~90 to 95% encounter rate for nesting turtles at Playa Grande and Sandy Point, respectively, there is only a nominal probability that a turtle would be missed in a given season. Thus, these tagging data provide an accurate representation of the number of nesting individuals each year.

Local air temperature and rainfall

Monthly air temperatures and rainfall for Playa Grande and Sandy Point were obtained from the Daniel Oduber Quiros International Airport (44 km from the nesting site) via the National Meteorological Institute of Costa Rica. For Sandy Point, these data were obtained from the Christiansted Hamilton Field Airport (10 km from the nesting site) via www.ncdc.noaa.gov/cdo-web/datasets/GHCNDMS/stations/GHCND:VQW00011624/detail. We calculated the mean monthly air temperature and total precipitation over the 6 mo nesting season.

Statistical analyses

We tested whether there had been a change in the MND, CT_{ns} , local air temperature, or local precipitation over the study period using least-squares linear regression. To compare the effects of ocean conditions before departure from foraging areas, ocean conditions during departure from foraging areas, ocean conditions during migration to nesting grounds, ocean condition on arrival at nesting grounds, and nesting population size on the MND and CT_{ns} , we used a generalized linear model with a Gaussian variance function and an identity link function. We compared these models using Akaike's information criterion (AIC). Data were analyzed using program R (R Development Core Team). For all statistical tests, $\alpha = 0.05$.

RESULTS

At Playa Grande between 1993–94 and 2012–13, the MND shifted to later in the season at a rate of approximately 0.31 d yr^{-1} , totaling a shift of 6 d (Fig. 1a). This shift was close to statistical significance ($r^2 = 0.17$; $p = 0.07$). The MND was highly variable with a range of 17 d. Much of this range was attributed to atypically late MNDs that occurred in 1993–94, 2002–03, and 2008–09. At Sandy Point, the MND shifted to earlier in the season at a rate of approximately 0.17 d yr^{-1} , totaling a shift of 5 d over 29 yr (Fig. 1c). While this shift was smaller than that at Playa Grande, it was statistically significant ($r^2 = 0.14$, $p < 0.01$). The total range of MNDs at Sandy Point was 14 d.

We found no significant correlations between the MND at Playa Grande and the MEI, yet there was a significant negative correlation between population size and the MND at Playa Grande ($p < 0.01$; Table 1, Fig. 2a). Furthermore, the AIC indicated that the best model for predicting MND included population size

as the only variable (see Table S1 in the Supplement at www.int-res.com/articles/suppl/n024p197_supp.pdf). No significant correlations were found between the MND at Sandy Point and the NAO, AMO, or population size (Table 1, Fig. 2b).

At both locations, the CT_{ns} showed no significant change (Playa Grande: $r^2 = 0.02$, $p = 0.53$; Sandy Point: $r^2 = 0.04$, $p = 0.32$; Fig. 1b,d). However, significant negative correlations were observed between the CT_{ns} at Playa Grande and the MEI during migration ($p = 0.03$) and the CT_{ns} at Sandy Point and the NAO during departure ($p < 0.01$; Table 1, Fig. 3a,b).

At Playa Grande, neither local air temperatures ($r^2 < 0.01$, $p = 0.77$) nor precipitation levels ($r^2 < 0.01$, $p = 0.97$) showed any significant changes over the study period (see Fig. S1 in the Supplement). The local air temperatures at Sandy Point decreased significantly ($r^2 = 0.28$, $p < 0.01$), but the observed decrease in precipitation levels was not significant ($r^2 = 0.04$, $p = 0.22$).

At both sites, there was a large change in the size of the nesting population over the study period,

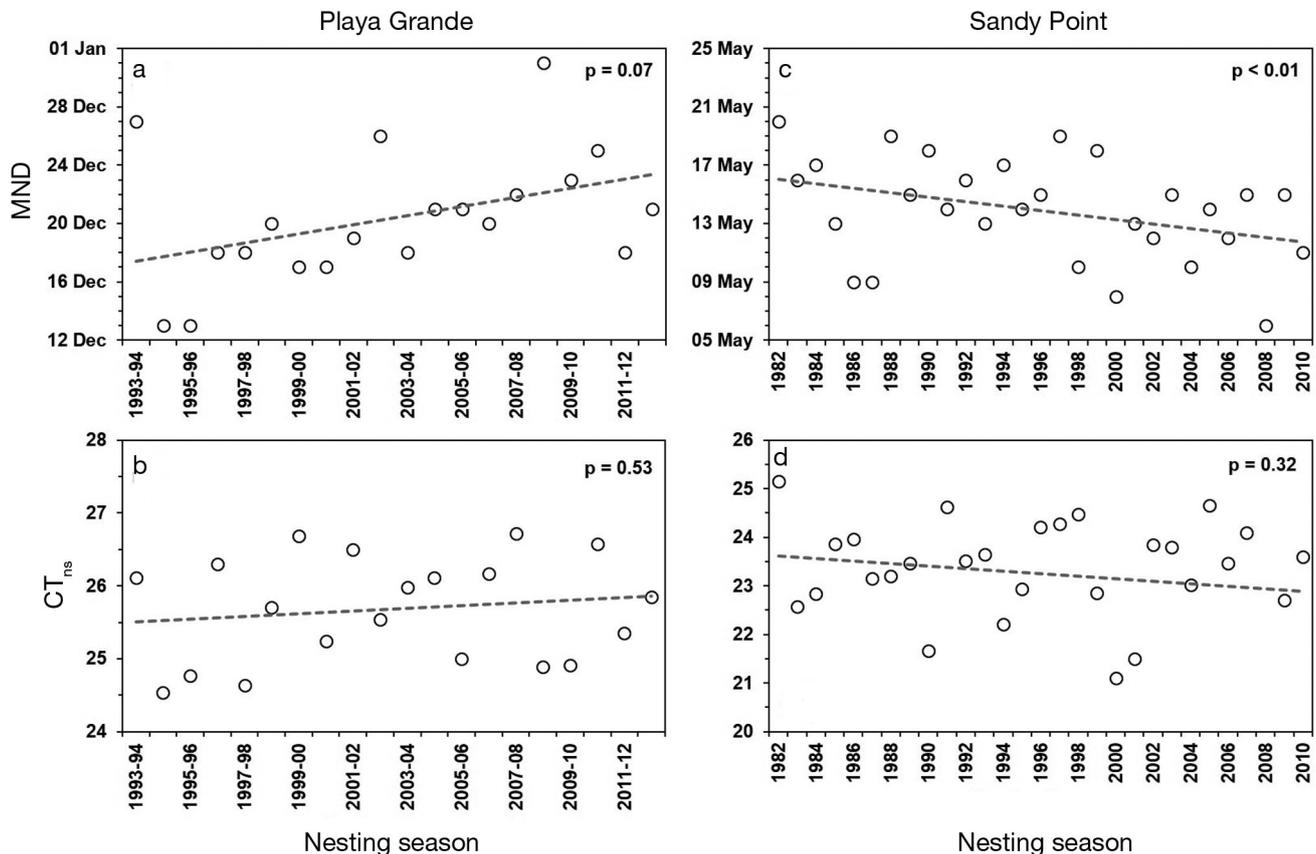


Fig. 1. Interannual trends in (a,c) the median nesting date (MND) and (b,d) the central tendency of the nesting season (CT_{ns} ; see 'Materials and methods: Nesting dates') for leatherback turtles *Dermochelys coriacea* at (a,b) Playa Grande, Costa Rica (Pacific Ocean) and (c,d) Sandy Point, US Virgin Islands (Atlantic Ocean). Dashed lines represent linear trend lines

which was evident beyond the substantial interannual fluctuations. The number of turtles nesting per year at Playa Grande decreased from ~300 at the beginning of this study to ~30 at the end. In contrast, the number of turtles nesting per year at Sandy Point increased from ~20 to ~150.

Table 1. Comparison of median nesting date (MND) and central tendency of the nesting season (CT_{ns} ; see 'Materials and methods: Nesting dates') for leatherback turtles *Dermochelys coriacea* at Playa Grande, Costa Rica (Pacific Ocean), and Sandy Point, US Virgin Islands (Atlantic Ocean), to oceanographic conditions using a generalized linear model with a Gaussian variance function and an identity link function. MEI: Multivariate El Niño-Southern Oscillation index; NAO: North Atlantic Oscillation index; AMO: Atlantic Multidecadal Oscillation index. Each index was averaged over periods that represented the time before departure from the foraging area, during departure from the foraging area, during migration between foraging and nesting areas, and upon arrival at the nesting areas. Asterisks (*) denote a significant correlation ($\alpha = 0.05$)

Variable	Playa Grande		Sandy Point			
	MEI		NAO	AMO		
	t	p	t	p	t	p
MND						
Before departure	-0.07	0.95	0.71	0.72	<0.01	0.93
Departure	0.50	0.63	0.06	0.06	0.02	0.45
Migration	-0.29	0.78	0.39	0.39	0.03	0.38
Arrival	-0.32	0.75	0.60	0.60	0.08	0.14
Combined	-0.30	0.77	0.94	0.94	0.07	0.15
Population size	-3.39	<0.01*	0.67	0.57		
CT_{ns}						
Before departure	-0.51	0.64	0.94	0.17	0.18	0.74
Departure	-1.03	0.32	0.43	<0.01*	0.12	0.93
Migration	-2.35	0.03*	0.37	0.10	0.21	0.62
Arrival	-1.96	0.07	0.14	0.99	0.12	0.94
Combined	-1.59	0.13	0.14	0.21	0.12	0.87
Population size	-1.93	0.07	1.05	0.41		

DISCUSSION

Here, we examined multidecadal trends in the nesting phenology of 2 populations of leatherback turtles inhabiting different ocean basins. To determine which factors govern nesting phenology for each population, we compared the observed trends in MND and CT_{ns} to ocean conditions experienced at different phases of migration as well as nesting population size. We also compared past trends in the MND to conditions at the nesting beach, to determine how such phenological changes may affect conditions for incubating nests. This information provided insights into the capacity of different leatherback turtle populations to adapt to future climate change through shifts in the timing of the nesting season.

Over the study period, the MND at Playa Grande occurred later, at a rate of 0.31 d yr^{-1} . In contrast, the MND at Sandy Point occurred earlier, at a rate of 0.17 d yr^{-1} . Such shifts in nesting phenology are relatively slow compared to other sea turtle species at higher-latitude nesting beaches (e.g. Weishampel et al. 2004, Pike et al. 2006, Mazaris et al. 2013). Moreover, the shift observed at Playa Grande is the first time a shift for nesting later in the year has been reported for any sea turtle population.

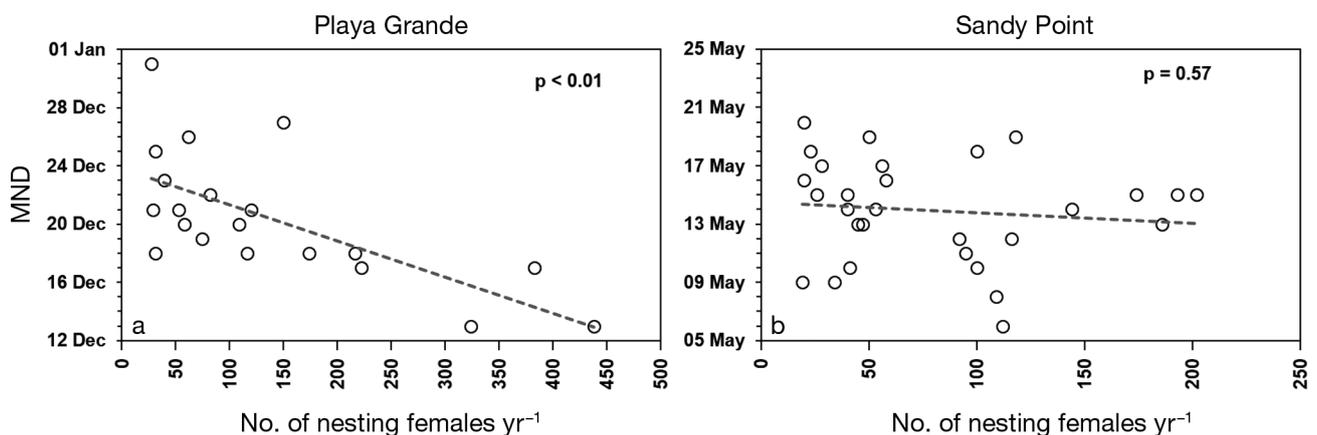


Fig. 2. Comparison of the median nesting date (MND) of leatherback turtles *Dermochelys coriacea* to nesting population size at (a) Playa Grande (Pacific Ocean) and (b) Sandy Point (Atlantic Ocean). Dashed lines represent linear trend lines

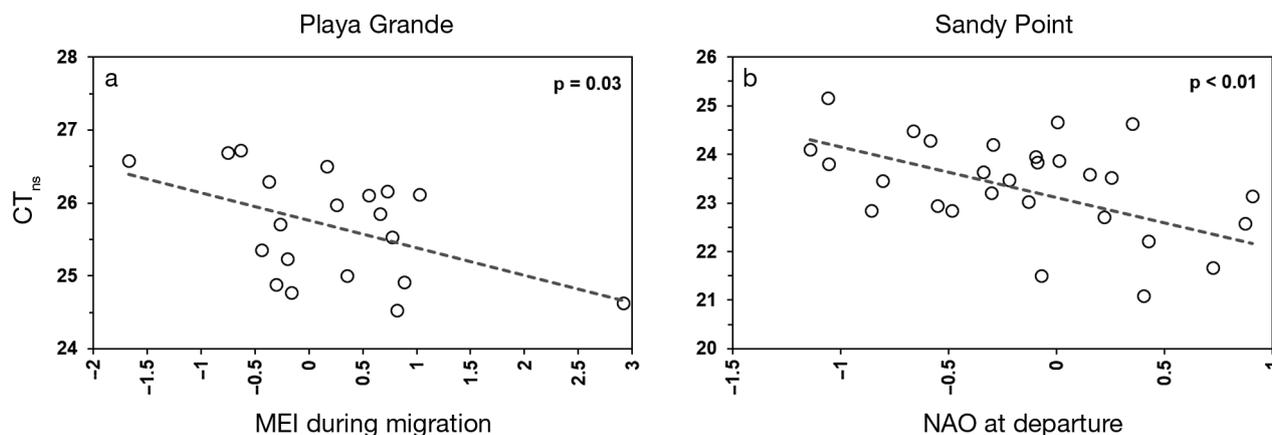


Fig. 3. Comparison of the central tendency of the nesting season (CT_{ns}) for leatherback turtles *Dermodochelys coriacea* and oceanographic conditions during specific sections of their post-nesting migrations. (a) At Playa Grande, the comparison between the contrary tendency of the nesting season and the multivariate El Niño-Southern Oscillation index (MEI) during the migration between foraging areas and nesting grounds is shown. (b) At Sandy Point, the comparison between the contrary tendency of the nesting season and the North Atlantic Oscillation (NAO) index during departure from the foraging areas is shown. Dashed lines represent linear trend lines

The strongest correlation with MND was observed between nesting population size and MND at Playa Grande. Although the shift in the nesting phenology at Playa Grande over time was not significant, this trend is likely to continue if the population continues to decline. In addition, no significant correlation was observed between population size and the MND at Sandy Point. We therefore hypothesize that the changes in nesting phenology may not be driven by population size specifically, but by changes in population demography. Specifically, the trends may be caused by changes in the ratio of younger and later nesting turtles to more experienced, and earlier nesting, turtles. Between the mid-1970s and early 1990s, approximately 90% of all the eggs laid at Playa Grande were poached (Santidrián Tomillo et al. 2008). As leatherback turtles are estimated to reach sexual maturity between 9 and 16 yr (Zug & Parham 1996, Jones et al. 2011), the resulting ‘missing’ generation should have begun nesting between the mid-1980s and early 2000s. Consequently, in 1993 at Playa Grande, the beginning of our study period, a large portion of the younger and later nesting individuals were absent. Yet over time, as the hatchlings from nests protected from poaching became reproductively mature, this younger generation of nesting turtles should again reappear in the population and this should shift the MND to later in the year. This shift in the average age of the population at Playa Grande may even be compounded by the increasingly high levels of adult mortality suffered by this population due to incidental take by fisheries (Spotila et al. 2000, Lewison et al. 2004), which would also reduce the av-

erage age of the population. In contrast, at Sandy Point, there has been a marked increase in the population of nesting leatherback turtles since the early 1980s (Dutton et al. 2005). As this increase was largely a product of increased recruitment into the population, the average age of the nesting population has probably remained low or only increased slightly, thus potentially explaining the lack of a correlation between population size and MND at Sandy Point.

At both Playa Grande and Sandy Point, we found no correlation between the MND and the MEI and NAO or AMO, respectively. Such results are surprising considering that oceanographic conditions have previously been linked to the departure date of pre-nesting leatherback turtles from their foraging areas in the waters of eastern Canada (Sherrill-Mix et al. 2008). However, that study investigated satellite-tracked individuals and thus was able to examine the oceanographic conditions directly at the animal’s location. In our study, we did not know the exact location of the turtles prior to nesting so we chose to use indices that provide a coarse-representation of ocean conditions over entire ocean basins, specifically the MEI, NAO, and AMO. Our decision to use such broad-scale oceanographic factors may have masked the actual effect of ocean conditions on the MND. Thus, we recommend that future studies attempt to focus their investigation onto areas within known high-use leatherback turtle habitats, such as the eastern portion of the South Pacific Gyre for turtles from Playa Grande (Shillinger et al. 2011) or the waters of eastern Canada for the turtles from Sandy Point (Fossette et al. 2010).

The only correlations we found between oceanographic conditions and nesting phenology were between the MEI and NAO and CT_{ns} of nesting season at Playa Grande and Sandy Point, respectively. Specifically, CT_{ns} at Playa Grande was negatively correlated with the MEI during the migration period, and CT_{ns} at Sandy Point was negatively correlated with the NAO during the departure period. Positive values of the MEI are generally associated with lower food availability for leatherback turtles in the Pacific Ocean (Saba et al. 2007, Reina et al. 2009), and similar patterns might also be true for the NAO in the Atlantic Ocean (Attrill et al. 2007). When less food is available to pre-nesting turtles, they might not be able to brood as many eggs and thus lay fewer clutches on arrival at the nesting grounds, leading to a shorter nesting season. Alternatively, if food is more patchily distributed then this could also lead to greater variation in departure dates and, in turn, also arrival dates.

CONSERVATION IMPLICATIONS

At both Playa Grande and Sandy Point, beach temperatures increase over the season (Santidrián Tomillo et al. 2009; see Fig. S2 in the Supplement). Consequently, nests laid later in the season are exposed to hotter and drier conditions and have lower hatching success and emergence rates (Santidrián Tomillo et al. 2009). At Playa Grande, where the nesting season is shifting to later in the year, this means that an increasing portion of the population will experience fatally hot and dry conditions and hatchling output will decrease. Even though no increase in local temperature has been recorded over the past 20 yr, declines in hatchling output are likely to be further exacerbated by future climate change (Santidrián Tomillo et al. 2012) as global temperatures are expected to increase by approximately 2°C before the end of this century (Stocker et al. 2013).

In contrast to the leatherback turtles nesting in Playa Grande, those nesting at Sandy Point may be able to better persist under conditions of climate change due to the observed shifts in nesting phenology. Indeed, so far the MND at Sandy Point is shifting towards cooler conditions at the beginning of the nesting season. Local air temperatures have even decreased over the past 29 yr. However, this does not mean that populations at Sandy Point are safe from the effect of climate change over long time scales. Shifts in nesting phenology may not continue indefinitely if they are ultimately controlled by demogra-

phy, and even the lowest seasonal temperatures will eventually rise if current trends persist with climate change.

If population demography does have a significant influence on nesting phenology, a method to facilitate beneficial shifts in nesting phenology may be possible. Specifically, conservation efforts that focus on reducing adult mortality may have the additional benefit of increasing the average age of the nesting population. More experienced, older individuals also tend to nest earlier and so this could shift the MND to earlier in the year. Yet it must be noted that the shifts observed in our study are small and, thus, shifts in nesting phenology may not be rapid enough to offset the future impacts of rapid climate change. Instead, the conservation of leatherback turtles, especially in the Pacific Ocean where populations are already severely depleted (Spotila et al. 2000, Tapilatu et al. 2013), may have to rely on additional proactive measures to reduce incubation temperatures for eggs through direct manipulation of environmental conditions, e.g. watering or shading nests (Patino-Martinez et al. 2012).

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