Phenological response of sea turtles to environmental variation across a species’ northern range

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Variations in environmental parameters (e.g. temperature) that form part of global climate change have been associated with shifts in the timing of seasonal events for a broad range of organisms. Most studies evaluating such phenological shifts of individual taxa have focused on a limited number of locations, making it difficult to assess how such shifts vary regionally across a species range. Here, by using 1445 records of the date of first nesting for loggerhead sea turtles (Caretta caretta) at different breeding sites, on different continents and in different years across a broad latitudinal range (25–39°N), we demonstrate that the gradient of the relationship between temperature and the date of first breeding is steeper at higher latitudes, i.e. the phenological responses to temperature appear strongest at the poleward range limit. These findings support the hypothesis that biological changes in response to climate change will be most acute at the poleward range limits and are in accordance with the predictions of MacArthur’s hypothesis that poleward range limit for species range is environmentally limited. Our findings imply that the poleward populations of loggerheads are more sensitive to climate variations and thus they might display the impacts of climate change sooner and more prominently.

1. Introduction

The influence of climate change has been studied for a variety of ecosystems and taxa, with scientists striving to reach a consensus regarding the possible responses of species. Geographical range shifts and seasonal changes in abundance and biological processes are the two most often cited responses of species to climate change [1–3]. Many studies demonstrate that species have shifted their geographical range to higher latitudes or altitudes in order to track the new geographical location of their climatic niche [1,4]. The thermal preferences and/or tolerances of a species often form a major component of its climatic niche. However, there are also examples of species that have not expanded or contracted their geographical range limits [5]. Numerous studies also reveal shifts in the seasonal timing of biological events, i.e. changes in phenology [1,6,7]. Such phenological responses include earlier flowering [8] in plants and earlier migration or reproduction in animals [3].

The response of populations and species to climate change is strongly linked to ecological and evolutionary processes [9]. Such processes rely on genetic adaptation and/or phenotypic plasticity [10,11]. Genetic adaptation refers to evolutionary adaptive responses of genotypes to local environment [12]. Phenotypic plasticity refers to the ability of a genotype to exhibit a range of phenotypes in response to specific environmental cues and could result in...
spatial and temporal variation in life-history features within and among populations without any genotype changes [13]. The degree of phenotypic plasticity across a geographical gradient could correspond to a gradient of environmental variation [14] or could be dominated by local conditions that are not part of a larger environmental gradient [15]. An understanding of phenological responses is important in order to predict the effects of climate change. However, few studies have examined how phenological changes vary across the range of broadly distributed species (but see [15–17]). Hence, it remains difficult to make generalizations about the patterns of phenological responses across the range limits of species. Theoretical work predicts that species’ phenological responses are unlikely to be uniform throughout their distributional range, with populations at the range limits behaving very differently [18–20].

Theoretical work has highlighted the role of ecological and evolutionary mechanisms, such as niche selection, dispersal, environmental variability and biotic interactions, in shaping species ranges [see (21,22)], but still the mechanisms and factors determining the limits of species ranges remain an open research question. Ever since 1972, MacArthur [23] has hypothesized that different mechanisms determine the poleward limit versus the equatorial limit. He postulated that the poleward boundary of a species’ range is set by direct environmental limitations, because the adverse environmental conditions may exceed the species physiological tolerance levels and thus restrict the species ability to survive. On the other hand, towards the equatorial boundary, environmental conditions are more productive and are less environmentally variable, thus they support heterogeneous habitats and are favourable for a wide array of species that interact with each other [23–25]. Therefore, the equatorial species range limit is set by biotic interactions (such as competition, predation and parasitism).

Sea turtles, as ectothermic species, have a nesting and reproductive ecology that is sensitive to environmental conditions. In addition, considering that sea turtles are a cosmopolitan group of species with only poleward range limits, one could suggest that if the long standing hypothesis of MacArthur [23] holds, the range limit of the species might be set by abiotic factors related to colder sea temperatures. This might become apparent when analysing the effect of climatic conditions (such as sea surface temperature, SST) on the phenology of the species, for example on the timing of reproductive events such as nesting. Under this point of view, the analysis of the sea turtle responses to SST inter-annual variation might serve as a test of MacArthur’s [23] hypothesis.

Because both ecological and evolutionary processes define the species geographical range, it is likely that the species response to environmental factors might be defined phylogenetically. For example in a recent study, Davis et al. [26] demonstrate that phenological responses to climate change for plants were phylogenetically biased, whereas no such clear pattern was obtained for birds. Phylogenetic relationships could drive common phenological shifts at geographically distinct communities [26] which might be determined by species traits such as metabolic capacity and body temperature that could in turn be driven by the interactions of phylogenetic similarities and climate [27]. Still, only few studies have so far explored any such relationship from a phylogenetic framework [28,29].

The loggerhead sea turtle (Caretta caretta) as a wide ranging species with nesting range distributed across temperate and subtropical coastal sites of the Atlantic, Indian, and Pacific Oceans and the Mediterranean Sea [30] could serve as a good model for examining how broad-scale latitudinal changes in phenology are linked to climate. Loggerhead turtles are ectothermic, with their terrestrial and oceanic life-history traits and behaviour strongly linked to temperature [31]. At the nesting beaches, sand temperature during incubation period determines hatching sex ratio, hatching success and incubation duration [32]. Sea temperature near nesting beaches is important in influencing local climate, i.e. air and sand temperatures further affecting incubation process. Sea temperature near the nesting rookery further affects the duration of the inter-nesting interval of females [33] potentially leading to faster egg formation [34]. The timing of the nesting season in combination with a change in the inter-nesting period could affect reproductive fitness of females and hence population growth. There is evidence that an increase in SST may affect nesting phenology, nesting behaviour and reproductive output in marine turtles [35–37]. Studying the links between nesting phenology and variations in present-day environmental parameters could provide some insights on the potential impacts of future climate change scenarios. In particular, studies have demonstrated a positive correlation between the onset of the nesting season and the temperature of sea water around the nesting rookery [38–40]. The studies that have analysed the effect of SST on the initiation of nesting considered only single nesting rookeries, located towards the northern end of the species’ range, mostly in high latitudes (greater than 28° N), raising a concern that the observed trends might be sensitive to site-specific conditions.

A separation between populations at the Indian-Pacific and the Atlantic–Mediterranean basins occurred approximately 3 Ma, according to studies on the evolution and global phylogeography of loggerheads [41]. Following these separations, new colonization events, geographical shifts and contractions, subdivisions and isolation of populations have occurred, which could be related to major climatic changes over geological time [37]. During periods of global warming, range expansions towards higher latitudes occurred, while during cooling events and changes in sea level, range contractions were observed [42]. It remains unclear whether current changes in environmental conditions are of such magnitude that they could drive similar responses.

We conducted a meta-analysis of loggerhead turtle nesting patterns using records from different breeding sites from the eastern United States (US) and Mediterranean to examine existing variation in phenotypic expression of traits (e.g. nesting phenology) in response to existing variations in environmental parameters that are thought to be affected by future climate change. We further divided our nesting aggregations into similar genetic stocks to examine whether the observed patterns are phylogenetically related. Our overall objective was to study the spatial and temporal complexity of varying climate conditions on nesting responses to determine whether systematic changes in phenology across the range of a species occurred. First, we examined whether increasing SSTs correspond with an advance in the onset of nesting. Next, we studied whether changes in the strength and/or magnitude of nesting phenological shifts demonstrated a latitudinal gradient correlated to
ambient temperatures. The findings of our study could distinguish which populations are more sensitive to climate variation, and thus identify which populations are more likely to be affected by future climate change, providing guidance for prioritizing conservation efforts in the context of climate change.

2. Material and methods

We compiled a dataset from literature sources (see the electronic supplementary material, SI), containing 1145 records of annual nesting activities reported at 223 nesting rookeries located along the eastern seaboard of the US and across the Mediterranean from 1980 onwards (from 1980 through to 2009). The sources used for compiling the data included research articles published in scientific journals and grey literature sources such as symposium proceedings, annual, inter-annual and regional monitoring reports but also Internet sources. In the present study, we analysed any record of loggerhead nesting activity at a given location, which was considered to be a distinct nesting site. All sites that were used in the present study have been reported as supporting nesting activity of loggerheads. The criterion for data inclusion was data availability and not the time period for which nesting activity has been recorded in the specific sites. The sites were distributed along the eastern seaboard of the US and across the Mediterranean, with the most southerly and northerly sites being located at 25° N and 39° N respectively, spanning a 1665 km latitudinal range (figure 1).

According to Wallace et al. [43], the nesting sites analysed in the present study belong to two distinct regional management units (RMUs; Mediterranean and the Northwest Atlantic). RMUs are defined as geographically explicit population segments determined by genetic studies, satellite telemetry data and tagging information. Considering that only a few loggerhead nesting activities have been reported at higher latitudes, our study area covers the northern poleward limit of the well-established nesting sites of the species.

All dates at the initiation of nesting activities, defined as the date of the first confirmed clutch laid on a beach in a given year, were presented as day of the year, starting from the first January with appropriate correction for leap years. In other studies, on sea turtle nesting phenology, authors have used other measures of nesting phenology, such as the median date of nesting period per year, for studying potential impact of environmental drivers such as SST [38]. However, each measure of nesting phenology has advantages and disadvantages. For example, the median date may decrease, even if the onset of nesting starts is delayed, if the end of nesting occurs considerably earlier. However, calculation of the median nesting date requires detailed datasets on nesting activity, which were not available and/or accessible for many nesting sites of our dataset. Because previous studies on loggerheads documented that SST affects the onset of nesting, we analysed the date of the first clutch laid, which seems to represent responses of members of the population to environmental cues.

Geographical position of each site was derived from the same data sources, by searching other published material on the specific nesting site, or by locating the coordinates of the nesting area from satellite images using Google Earth. We further compiled data on the total number of nests produced at each nesting site in a given year. For more than 75 per cent of the records (n = 871), we were able to compile data on last nesting date, defined as the last confirmed clutch laid in a given year, which allowed us to estimate the duration of the nesting period.

Loggerhead nesting in the Northern Hemisphere regularly starts in April to May each year [30]. Monthly average SST data for the nesting sites were derived from an extended reconstructed sea surface temperature (ERSST) dataset available with a 1° global spatial resolution from the National Oceanic and Atmospheric Administration of USA (http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.ersst.html). The ERSST dataset presents global SST time series based on in situ and
satellite-derived observations coupled with sea-ice concentrations [44]. To extract SST data, we selected the 1° grid cells that encompassed the coordinates of each nesting site; these grid cells extending a maximum of 111 km out to sea. Gravid female loggerheads are expected to use an area of a few kilometres around their nesting sites, which will fall within the 1° grid cells provided by the ERSST dataset. The SST data used for each nesting site refer to the same time period as the respective nesting data for the specific beach.

Simple and multiple linear regressions were used to investigate for potential relationships between SSTs and the onset of nesting. All correlation analyses for latitudinal trends were corrected using the modified Clifford \(t\)-test that accounts for spatial autocorrelation by using Morans’ \(I\)-test and corrects accordingly the degrees of freedom [45].

To consider if the observed correlations between nesting phenology and SST were confounded by population density, we examined whether the residuals of the phenology versus SST relationships were related to the total number of nests produced in a season. Our results however, showed this correlation to be not significant (after correcting for spatial autocorrelation, \(p = 0.852\)).

To investigate whether the observed patterns could be driven by genotypic differences across different sites, we aggregated data on nesting sites according to genetically defined nesting stocks (both on the US Atlantic coast and in the Mediterranean) and we re-analysed the patterns using latitude as our only parameter. Information on genetic stocks was derived by the SWOT database (http://seamap.env.duke.edu/swot) [43,46], with distinct genetic stocks globally determined based on maternally inherited mitochondrial DNA patterns that differentiate population structures [46]. In our study area, we identified a total of seven distinct genetic stocks out of the 15 that have been identified for loggerheads worldwide (four in the US Atlantic coast and three in the Mediterranean; however, we have insufficient data for two of the Mediterranean stocks and these were omitted from the analysis).

3. Results

In our dataset, the earliest onset of nesting was on 7 April observed in 1990 on Miami nesting beach, Florida, and the latest on 30 June recorded in Cape San Blas, Gulf County, Florida. For the combined data of both Atlantic and Mediterranean basins, the mean date of first nest was day 136.8 ± 15.0 (median = 136), corresponding to 16 May. Across the latitudinal range examined, earlier nesting occurred further south and later nesting occurred further north. For example, at latitudes of 26°N and 36°N, the mean dates of the first nests were day 128 (±13) and day 150 (±8.5), respectively, demonstrating significant differences (Mann–Whitney \(U\)-test, \(p < 0.01\)).

Across the 1145 records of first nesting, there was a significant negative relationship between April SST and first nesting dates (Clifford \(t\)-test = \(-0.126, p < 0.05\)). The negative effect of April SST upon all records of first nesting dates was maintained (\(b = -1.778, p < 0.01\)) even when including latitude as a predictor variable (\(b = 0.698, p < 0.01\)) by means of multiple regression (\(r^2 = 0.125, p < 0.01\)). Similar trends were obtained when analysing Mediterranean and west Atlantic data separately. To investigate whether there is a SST threshold that could trigger the onset of nesting, we compared SSTs at the time of first nest at each nesting site regardless of the actual date, but we found that no such clear SST metric existed, with SSTs differing significantly among the nesting sites (\(p < 0.01\)). Overall, mean April SSTs at the time of first nesting was strongly and significantly associated with latitude (\(r^2 = 0.96, p < 0.01\)). Nesting begins under higher SSTs at lower latitudes. The range of April SSTs at which onset of nesting occurred varied between 16.7°C and 25.6°C, with extreme temperatures reported at latitudes 39°N and 20°N, respectively.

We ordered studies by grouping them into cells of a similar physical size (i.e. 1° latitude × longitude) and found a significant positive correlation between mean date of first nesting and latitude (\(r^2 = 0.154, d.f. = 43, p < 0.01\); figure 2). When we regressed the earliest recorded nesting date for each 1° cell, the trend became even stronger supporting a clear latitudinal gradient (\(r^2 = 0.504, d.f. = 43, p < 0.01\); figure 2). The mean date of first nesting was also significantly negatively associated with mean April SSTs across the species nesting range (\(r^2 = 0.213, d.f. = 43, p < 0.01\), with the trend being stronger when regressing the earliest nesting date per 1° cell (\(r^2 = 0.484, d.f. = 43, p < 0.01\); figure 3).

To examine whether there were regional variations in the nature of the relationship between date of first nesting and
April SST, we analysed trends in data pooled into 1° latitudinal bands for different ocean basins and we considered only time-series that had at least 10 years of data (n = 11 sites). Conveniently, these bands spanned 11° of latitudes, with mean nesting date being strongly and significantly correlated with mean April SSTs ($r^2 = 0.951$, d.f. = 10, $p < 0.01$). For example, figure 4 shows this relationship for data on the onset of nesting collected across the latitude of 26°N and 36°N and April SST. At the more southerly site, the relationship between the date of the first nest and April SST was not significant ($r^2 = 0.0023$, d.f. = 69, $p = 0.692$), and the slope was close to zero. At the more northerly site, the relationship was significant ($r^2 = 0.384$, d.f. = 13, $p < 0.05$) with a relatively steep slope: a 1°C increase in April SST was associated with the mean date of the first nest advancing by 6.4 days. We repeated this analysis for all 11 sites with extended time series and found a general pattern for the slope of the first nest versus April SST relationship to be significantly correlated with both latitude ($r^2 = 0.759$, d.f. = 10, $p < 0.01$; electronic supplementary material, II) and April SSTs averaged over the years of observations ($r^2 = 0.763$, d.f. = 10, $p < 0.01$; electronic supplementary material, III).

We further grouped the nesting sites according to genetically defined nesting stocks by deriving data from the SWOT database [43,46]. The analysis that was performed on the few genetic stocks demonstrated a significant negative relationship between mean April SST at the time of first nesting and mean latitude of these stocks ($r^2 = 0.989$, d.f. = 4, $p < 0.01$; electronic supplementary material, SIII). Although no significant association was detected between the mean date and the earliest recorded nesting and latitude (in both cases $p > 0.05$), we found that the slope of the first nest versus April SST relationship to be significantly correlated with latitude ($r^2 = 0.815$, d.f. = 4, $p < 0.05$) and April SST ($r^2 = 0.795$, d.f. = 4, $p < 0.05$). We found no significant correlation between the range of April SSTs measured across years at each site and the gradient of the first nesting date versus April SST relationship ($p = 0.13$). Warm southerly sites could have a marked inter-annual variation in April SST, but still not have a strong relationship between the date of the first nest and April SST.

The duration of the nesting season was negatively associated with the first nesting dates ($r^2 = 0.572$, d.f. = 870, $p < 0.01$) and positively associated with April SSTs ($r^2 = 0.015$, d.f. = 870, $p < 0.01$), indicating that earlier onset of nesting is associated with a longer nesting season. The duration of the nesting season was weakly but significantly negatively correlated with latitude ($r^2 = 0.012$, d.f. = 870, $p < 0.01$), indicating shorter nesting seasons at higher latitudes. The total number of nests produced per site annually was not significantly correlated with either April SST ($r^2 = 0.0003$, d.f. = 1144, $p = 0.511$) or the residual variation of the relationship between first nesting dates and April SST (after correcting for spatial autocorrelation, $p = 0.852$).

When the analyses presented above were also conducted using March SSTs and the average across consecutive months (i.e. March, April and May), the results qualitatively remained the same, i.e. the previously mentioned significant relationships remained significant and vice versa. The strongest correlations observed are those with April SSTs presented above.

4. Discussion

Our results show that for a species which breeds over a wide geographical range, nesting phenology is sensitive to environmental temperature, but that this link with temperature is not homogenous throughout the species range. Loggerhead turtle populations at high latitudes (i.e. the northern poleward boundary of the species’ range) were significantly and strongly affected by inter-annual variability in spring SSTs, with earlier onset of nesting in warmer years. At low latitudes, loggerhead turtle populations were less strongly affected by inter-annual variation in spring SST. Our results indicated a latitudinal trend, with an increase in latitude being associated with an increase of the strength and slope of the relationship between SST and nesting phenology. In addition, the extent of inter-annual variability in temperature was found to be similar across this range extent (see the electronic supplementary material, SIV), suggesting that the lack of a phenological response at low latitude was not simply a consequence of a lack of inter-annual variability in temperatures. Our results suggest that previous work [38–40] within the central part of species’ ranges, focused on rather fine spatial scales thus are not indicative of all populations, especially those located at the poleward range limits. In this sense, previous work may have underestimated the true extent of phenological shifts at range limits and hence our ability to distinguish the heterogeneous responses of biological organisms to environmental stimuli like climate change. To the best of our knowledge, there are limited similar published studies on the latitudinal patterns of the effects of climate change on the phenology of amphibian and/or reptiles with which to compare our findings. Phillimore et al. [15] showed that frogs across the UK spawn earlier in warmer years. In a similar study on birds, Both et al. [17] showed consistent phenological responses in nesting dates for flycatchers across Europe and the inter-annual differences in nesting dates were most marked at sites that experienced greater inter-annual variability in spring temperatures. Extending the conclusions drawn from these studies with other taxa, with our results for sea turtles,
we argue that it is not only the extent of inter-annual variability in temperature, but also the position of the breeding site within the species range that drives the magnitude of phenological response.

In the present study, biotic interactions were not studied, thus no conclusions can be drawn about the part of the MacArthur [23] hypothesis regarding the boundary towards the equator (i.e. on the role of biotic interactions in setting the species’ range limit in the tropics). Still, our results lend support to the part of MacArthur’s hypothesis regarding the environmental limitation of the poleward boundary of distributional ranges. Loggerhead populations at the northern poleward edge of their range (i.e. high latitude) seem to be limited by low summer SSTs that offer a relatively shorter optimal temperature window for nesting [47], and when the SSTs increased, the population took advantage of the improved conditions and the increased window of optimal environmental conditions, and started laying clutches earlier. Based on our results, we suggest that the mechanism responsible for earlier nesting may be primarily related to the optimal thermal window, which however may vary for different populations located along the latitudinal gradient. Such an optimal thermal window could be linked to resource allocation and acquisition; therefore, it could be influenced by ecological conditions and the organism’s physiological needs. In turn, such properties could also affect the optimal window; e.g. Schofield et al. [48] showed that Mediterranean turtles demonstrate preferential mechanisms towards selecting warm water patches and thus initiate nesting at an earlier date, resulting in a reduction of the time spent on the nesting grounds, thus minimizing of the time away from the foraging areas. Furthermore, given that the range of SSTs differs greatly for different latitudes, we were unable to identify a common temperature threshold that triggers onset of nesting over the latitudinal gradient of our study. Still, we suggest that when detailed, daily SST data becomes available, it might be possible to identify this thermal window, which would be very informative for understanding local population responses to environmental variations.

The patterns of phenology we observed may potentially be driven by behavioural plasticity of individuals depending on their nesting site and/or by natural selection driving genotypic differences across different sites. Distinguishing between these possibilities is not straightforward [49]. Certainly, there are some genotypic differences between individuals from spatially separated rookeries in most sea turtle species [50], though whether these differences underlie the varying phenological responses we observed is unclear. While individual female loggerhead turtles do have a general fidelity to nest in one area, they do occasionally move to breed on alternative sites [51,52]. It might be possible to track the breeding periodicity of individuals across years and across sites to disentangle the roles of phenotypic plasticity and genotypic differences in driving the observed spatial patterns of breeding phenology. Our results on genetically distinct nesting populations suggest that there is a latitudinal gradient of phenological responses to SST in the nesting stocks analysed. This finding implies that despite the existence of genotypic differences between distinct genetic stocks, the pattern for the correlation between the slope of the onset of nesting versus April SST relationship and both latitude and April SSTs might be a general trait of the species, with genetic stocks at higher latitudes demonstrating a steeper gradient of change. Still, we caution that this analysis was based on datasets from a limited number of genetically distinct stocks [43]; therefore, we strongly suggest that more data on genetically defined nesting stocks would improve our understanding on species responses.

In another case, Phillimore et al. [15] argued that in the case of the common frog (a species with a short lifespan compared with loggerheads), changes in breeding date with temperature were stronger when compared across sites rather than within individual sites. This lack of strong phenological changes within sites could suggest that behavioural plasticity did not underlie these observations, but rather they were caused by genotypic differences resulting from local adaptation [15] or alternatively, it could reflect a strong physiological plasticity across sites. Conversely, Chevin & Lande [14] have predicted that a higher degree of plasticity could be expected at the edges of a species geographical range. Our analyses showed a very strong response of both the onset and duration of nesting seasons to April SSTs, inter-annual variations in phenology strongly linked to SST in high latitude populations (i.e. at the species range) and a weak response at low latitude populations, reflecting a gradient in the species responsiveness to climatic stimuli variations. For the low latitude populations, Weishampel et al. [38] demonstrated a significant phenological shift of the median date of nesting in Melbourne Beach Florida (latitude approx. 28° N) in response climate change. This finding in association with our finding that the onset of nesting was not significantly affected by SST at low latitude, might imply that the shift in the median day could be owing to a shorter duration of the nesting season in this case.

We also considered the possibility that population nesting density might confound the observed correlations between nesting phenology and SSTs that could introduce a source of bias in the observed trends [53]. It might be expected that the size of a nesting population might also influence the date of the first and last nests of a season [53–55]. For example, if two populations have the same mean nesting date and associated standard deviation (i.e. two populations have the same distribution of nesting activity), then if one population is larger, it is more probable that the extremes of the distribution are observed. However, no impact of population size, by means of the number of nests laid, was detected suggesting that SST is the most important driver of the phenological responses across sites. In any case, we caution that the metric of population size that was available and was analysed here was total number of nests per site. The complex relationship between SSTs and inter-nesting periods in sea turtles could have affected the total numbers of nests per season at each site. Therefore, although we used the total number of nests per site as an indicator of population size, the total number of nesting females per season but also the distribution of clutch frequencies among nesting females could serve as more useful metrics of population dynamics and help interpret our results. Climate change scenarios predict that SSTs will increase and hence we could argue that the response of the low latitude nesting populations could possibly be indicative of how high latitude loggerhead populations might respond to climate change in the future. That is, as SSTs increase at higher latitudes, then the high latitude populations might eventually show responses more like today’s low latitude populations; i.e. nesting phenology linked to SSTs but insensitive to
strong inter-annual variations. A possible explanation for this ‘insensitivity’ to large inter-annual variations at low latitudes might be that the (albeit wide) range of SSTs at low latitudes generally span the temperature preference window for loggerheads. The sensitivity at high latitudes might be owing to the lower range of the SSTs observed falling outside of the preferred temperatures and thus acting as a constraint on species behaviour.

The advances in nesting phenology could be considered as one of the most pervasive consequences of climate change on sea turtles [36–40]. However, trying to predict the wider implications of climate change on loggerhead turtles is not an easy task. During a nesting season, sea turtles lay several clutches of eggs with the average inter-nesting interval reduced under increased SSTs [33]. Therefore, an extension of the nesting season along with a reduction of the inter-nesting interval may potentially increase the number of clutches laid per breeding season in warmer conditions. This scenario is perhaps most likely to occur at high latitudes where the shorter nesting seasons mean that the reproductive output of individuals is less likely to be limited by body stores. These interactions illustrate the possibility that loggerhead turtles may be able to capitalize on climate warming by increasing reproductive output at their range limits. A plausible increased reproductive output in the high latitude populations might be indicative of a greater availability of individuals at the poleward range limit to disperse towards higher latitudes where currently environmental conditions are not suitable but that will become suitable after climate change. This increased availability of dispersers might allow the faster shift of geographical range, as has been theoretically shown [18]. However, we should also consider the possibility that other factors might create a barrier towards a range shift. Geographical nesting patterns in loggerheads appear to be constrained by the proximity to oceanic currents that facilitate the offshore migration of hatchlings [56], or the increased sea levels may squeeze the available space for nesting [57]. If oceanic conditions are less favourable for hatching migration at more poleward sites a range shift would be impeded. As the climate continues to change, continued monitoring and reporting of breeding phenology and nesting numbers may shed light on these possible scenarios. Still, given that much research into potential effects of climate change on sea turtles has focused on nesting beaches, a better understanding of how oceanographic features and conditions affect sea turtle marine life history is needed.

In any case, we caution that even longer nesting seasons are not necessarily associated with higher reproductive output. It needs to be tested whether poleward populations compensate for shorter nesting seasons (i.e. fewer clutches) by increasing clutch size (i.e. number of eggs per clutch), thus negating any consequences for reproductive output owing to shorter nesting seasons. We should also consider that inter-annual variation in nesting abundances could be linked to conditions on foraging grounds [36,58] further influencing inter-annual variation in nesting phenology. As a result, a temporal lag in nesting abundances could be obtained among and within a nesting site through time. But even if conditions on foraging grounds might influence reproductive phenology (and mainly the remigration interval), the effect on nesting dates is considerably less than SSTs at the breeding grounds [36].

Overall, our study area covers the northern poleward limit of the well-established nesting sites of the species. Still, some major nesting occurs at the Northern Hemisphere nearer the equator, i.e. the Cape Verde Islands in the Atlantic Ocean and Oman in the Indian Ocean. In addition, loggerhead nesting also occurs in the Southern Hemisphere (Brazil, South Africa and Australia), albeit within broadly the same latitudinal range from the equator. Hence, although our study is likely to largely cover the range of thermal conditions experienced at loggerhead rookeries across the northern loggerhead range, we strongly encourage similar studies at the southern range of species range and at the sites located nearer to the equator, to produce a more complete picture of population responses to environmental changes.

Given the importance of investigating the impacts of climate change upon species’ behaviour and population dynamics, the challenge is to provide predictions for the future of the species. We should caution against over-dramatizing the purportedly drastic impacts of climate change on sea turtles. Our results highlight that the species response to existing variations in environmental parameters that are thought to be those sensitive to future climate change scenarios are heterogeneous and not all populations face the same threat level. Populations located towards the poleward boundary of the species range are more strongly affected. Thus, priority should be given for research and monitoring of these populations that would display the effects of future climate change sooner and more markedly.

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