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THE IMPACTS OF CLIMATE CHANGE ON SEA TURTLES, AND METHODS TO ASSESS POTENTIAL CHANGES IN NESTING PHENOLOGY

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INTRODUCTION

Anthropogenic climate change is one of the primary threats to the environment and human society (Pecl *et al*., 2017; Lenton *et al*., 2019). This planetary-level modification has had unprecedented effects on ecosystems and biodiversity (Newson *et al*., 2009; Walther, 2010). Numerous species have already demonstrated alterations in their distribution and phenology, amongst other responses (Walther, 2010; Feeley *et al*., 2017; Piao *et al*., 2019). For example, mobile species like tropical fish have responded to climate change by migrating to more habitable regions, usually poleward or to deeper water, in order to find their preferred range of oxygen availability or water temperature (Munday *et al*., 2008). Milder winters have caused a significant increase in brown plumage in populations of tawny owls, allowing them to blend in better with the surrounding forest, in Europe (Karell *et al*., 2011). Moreover, fruit flies in southern, high-latitude areas of Australia are demonstrating genetic mutations common to more northern populations of the country as the species has adapted to drier and hotter conditions. Scientists have attributed these changes to climate change and have observed similar trends in Europe and North America as well (Umina *et al*., 2005).

Sea turtles are another taxon likely to be affected by climate change, across all their life stages. The predicted impacts include:

1. Sex ratios: As sea turtles have temperature-dependent sex determination, increase in incubation temperatures at nesting beaches may result in the feminisation of some populations (e.g., Janzen, 1994; Santidrián Tomillo *et al*., 2015a; Jensen *et al*., 2018) and decreased egg fertilisation rates (Glen & Mrosovsky, 2004; Lalöe *et al*., 2014; Jensen *et al*., 2018; Phillott & Godfrey, 2020).
2. Embryo development: Embryo development is faster at higher temperatures, reducing the incubation

period and allowing less time for embryo growth (Reid *et al.*, 2009). The result is smaller hatchlings, with implications for predation rates and performance.

3. Hatching success: Even small increases at the upper range of incubation temperatures can negatively affect hatching success (the proportion of eggs that hatch to produce hatchlings; Miller, 1999). For example, an increase from 30°C to 31°C mean incubation temperature can decrease hatching success by up to 25% (Howard *et al.*, 2014). Changes in average precipitation may also affect hatching success (Santidrián Tomillo *et al.*, 2012; Rafferty *et al.*, 2017; Montero *et al.*, 2018), with heavy rainfall increasing hatching success at drier nesting sites and the opposite or variable effects occurring at high-precipitation sites. (Santidrián Tomillo *et al.*, 2015b; Montero *et al.*, 2019). Lower hatching success will have implications for population recruitment and resilience.
4. Hatchling survival and performance: As incubation temperatures increase above 32°C, hatchlings perform more poorly on tests to assess their crawling, self-righting, and swimming abilities. Decreased locomotor performance at sea will make hatchlings more vulnerable to predation (Booth, 2017, 2018).
5. Movements and distribution at sea: Being ectothermic, sea turtles are affected by seawater temperature (Milton & Lutz, 2003). For example, Kemp's ridley (*Lepidochelys kempii*) turtles that disperse further north to forage with warmer sea surface temperatures (SSTs) during autumn months, then retreat too slowly from cold waters in winter, are at greater risk of cold-stunning (Griffin *et al.*, 2019). Some populations are already adapting to changing ocean temperatures, such as Eastern Pacific olive ridley (*Lepidochelys olivacea*) turtles that forage more northwards during an El Niño year to avoid warm waters and seek more productive upwelling areas (Plotkin, 2010), and hawksbill (*Eretmochelys imbricata*) turtles in the Arabian/Persian Gulf that move out of shallow, coastal foraging areas during the summer months when aquatic temperatures exceed 33°C (Pilcher *et al.*, 2014; Marshall *et al.*, 2020).
6. Reproductive output: The size of adult hawksbill turtles in the Arabian/Persian Gulf and Red Sea may be restricted by relatively poor foraging habitat and/or success due to extreme thermal environments. A smaller body size will limit clutch size in nesting females (Chatting *et al.*, 2018; Mobaraki *et al.*, 2022). There are indications that the number of yolkless eggs, comprising only an eggshell and egg white or albumen, laid by hawksbill turtles in these extreme environments are greater than that in other populations worldwide; the statistical likelihood and biological implications of this have yet to be determined (Mobaraki *et al.*, 2022).
7. Nesting habitat: Many current nesting beaches utilised by sea turtles will likely be reduced in area by sea level rise, with beaches in developed regions being the most vulnerable (Fish *et al.*, 2005; Baker *et al.*, 2006; Fuentes *et al.*, 2010). Coastal development can prevent the natural movement of sediment to replenish beaches, causing coastal squeeze, thus, exacerbating the impacts of sea level rise (Fish *et al.*, 2008; Mazaris *et al.*, 2009a; Biddiscombe *et al.*, 2020).
8. Geographic range: In response to climate change, sea turtles may shift their nesting (Mancino *et al.*, 2022) and foraging (Patel *et al.*, 2021) habitat. Range shift in the form of range expansion (as opposed to contraction), that exposes sea turtles to greater human activities, lesser quality habitat, and other threats, could form an ecological trap (Pike, 2013; Maffucci *et al.*, 2016). Range shift could also be beneficial, although thoroughly validated examples have not yet been reported in the published literature.
9. Emerging diseases and pathogens: Outbreaks of infectious diseases in some marine taxa have increased in the last few decades, likely driven by anthropogenic climate change (Fisher *et al.*, 2012; Altizer *et al.*, 2013; Sanderson & Alexander, 2020). In sea turtles, warmer waters could increase the rate of tumour growth in animals with fibropapillomatosis (Herbst, 1994, 1995; Foley *et al.*, 2005) and the pathogenicity, transmission pathways, and host susceptibility in any disease (see Mashkour *et al.*, 2020). The association of climate change with emerging diseases in the terrestrial environment, such as sea turtle egg fusariosis (Gleason *et al.*, 2020), has not been conclusively determined. Loss of nesting area with climate change-driven sea level rise will likely increase nest density (Patricio *et al.*, 2019) with implications for microbial load in sea turtle nests (Honarvar *et al.*, 2016) and the spread of pathogens among adjacent clutches (Sarmiento-Ramirez *et al.*, 2017). Foraging habitats, including seagrass meadows (Sullivan *et al.*, 2018) and coral reefs (Precht *et al.*, 2016; Tracy *et al.*, 2019), may also be impacted by disease and/or pathogens.
10. Nesting phenology: Alterations in the timing

of seasonal activities among animals and plants is a commonly observed ecological response to environmental perturbations like climate change (Walther *et al.*, 2002). Oceans have absorbed ~80% of the heat added to the environment (IPCC, 2007), impacting parameters like sea surface temperature (Hoegh-Guldberg *et al.*, 2007), biogeochemical composition (Harley *et al.*, 2006), and sea level (Meehl *et al.*, 2005). Ocean temperature affects the onset of nesting, duration of the nesting season, nest abundance, clutch size, mean nesting date, and other parameters of the nesting phenology of loggerhead (*Caretta caretta*) sea turtles in Florida (Lamont & Fujisaki, 2014). However, patterns are not always consistent. For example, higher annual SST adjacent to nesting beaches (Weishampel *et al.*, 2004, 2010; Pike *et al.*, 2006; Hawkes *et al.*, 2007; Mazaris *et al.*, 2008, 2013; Lamont & Fujisaki, 2014; Patel *et al.*, 2016) and at foraging sites (Mazaris *et al.*, 2009b, Monsinjon *et al.*, 2019) have both been correlated with earlier nesting. Longer (Weishampel *et al.*, 2010; Lamont & Fujisaki, 2014) and shorter nesting seasons (Pike, 2009; Weishampel *et al.*, 2010), and reduced inter-nesting intervals (Weber *et al.*, 2011; Valverde-Cantillo *et al.*, 2019), have been recorded in warmer years. Higher SST at nesting locations has also been associated with fewer total clutches, primarily as a result of fewer turtles nesting (Mazaris *et al.*, 2009b; Reina *et al.*, 2009; Patel *et al.*, 2016). Earlier nesting is predicted to mitigate exposure of eggs to lethal temperatures (Almpanidou *et al.*, 2018) and strongly female-biased sex ratios (e.g., Abella Perez *et al.*, 2016) that are predicted to occur with higher environmental temperatures due to climate change.

We note that the El Niño-Southern Oscillation (ENSO) and North Atlantic Oscillation are known or predicted to affect nesting in some sea turtle populations (e.g., Limpus & Nicholls, 1988; Chaloupka *et al.*, 2008; Saba *et al.*, 2008; Quiñones *et al.*, 2010; Mortimer, 2012; Arendt *et al.*, 2013; Bruno *et al.*, 2020; Santidrián Tomillo *et al.*, 2020; Hays *et al.*, 2022) but not others (Ariano-Sánchez *et al.*, 2020; Santidrián Tomillo *et al.*, 2020; Hays *et al.*, 2022). However, the impact of climate change on ENSO is still uncertain in the face of contradictory findings (e.g., Yang *et al.*, 2018; Alizadeh, 2022; Geng *et al.*, 2022); therefore, we do not include this in the above list.

The impacts of climate change on sea turtles, and its mitigation, were identified as a priority research area to inform conservation and management of sea turtles by Hamann *et al.* (2010). Subsequent reviews examined topics on which research has focused at a global scale, and found a growing body of knowledge, predominantly in the terrestrial phase of the sea turtle life cycle (Rees *et al.*, 2016; Patricio *et al.*, 2021). However, recent regional reviews found the impacts and/or mitigation of climate change on sea turtles were not well studied in the northwestern Indian Ocean and the east coast of Africa despite it being regarded by experts as an increasing threat (Al Ameri *et al.*, 2022; van de Geer *et al.*, 2022).

While studies on all the potential impacts of climate change on sea turtles deserve attention, understanding how nesting phenology may be affected is important, as changes in timings of migration and the onset and duration of nesting have the potential to exacerbate or mitigate the impacts of climate change (Pike *et al.*, 2006; Mazaris *et al.*, 2008; Pike, 2009; Weishampel *et al.*, 2010; Patel *et al.*, 2016). For example, the timing of the nesting season has implications for the exposure to climatic conditions and hatching success (Santidrián Tomillo *et al.*, 2012) and offshore currents facilitating hatchling dispersal and in-water survival (Shillinger *et al.*, 2012; Le Gouvello *et al.*, 2020). Hence, we conducted a systematic review of methods used worldwide in published studies examining alterations in sea turtle nesting phenology with climate change, e.g., changes in sea surface temperature, to identify the most common methods of collecting data and the variables examined. The findings of the review can inform and guide researchers in the Indian Ocean and Southeast Asia region (and beyond) who are interested in monitoring potential changes in nesting phenology at their study site/s.

METHODS

Google Scholar was used as the search engine to identify empirical studies, based on primary data, on the research topic. We performed a literature search using the key words/phrases "sea" OR "marine" AND "turtle" AND "nesting phenology". The search was restricted to literature published in peer reviewed journals and professional newsletters (e.g., Indian Ocean Turtle Newsletter, Marine Turtle Newsletter) to date in the 21st century (2000-2021). Results were screened through 1) review of title and abstract; then, 2) review of methods and results for relatedness to the research topic. The reference list of relevant literature was also examined to identify further studies pertinent to the topic that had not been identified through the search on Google Scholar.

After close reading of the texts, common themes and categories of data of interest were identified (emergent coding). Data about the focus species, geographic region, study objective, source and collection frequency of environmental data, metric/s of sea turtle nesting phenology, and finding/s were extracted from each paper and descriptive statistics used to summarise the proportion of studies within each code.

RESULTS AND DISCUSSION

From a total of 407 search results, filtering identified 15 publications that met our criteria and were included in the systematic review: Weishampel *et al*. (2004, 2010), Pike *et al*. (2006), Hawkes *et al*. (2007), Mazaris *et al*. (2008, 2009b, 2013), Pike (2009), Hassine *et al*., (2011), Dalleau *et al*. (2012), Lamont & Fujisaka (2014), Neeman *et al*. (2015), Patel *et al*. (2016), Monsinjon *et al*. (2019), and Valverde-Cantillo *et al*. (2019). All examined changes in nesting phenology in association with SST.

Loggerhead (73.3%) and green (*Chelonia mydas*; 26.7%) turtles were the subject of all but one of the nesting phenology studies examined. No studies considered flatback (*Natator depressus*), hawksbill, Kemp's ridley, or olive ridley turtles (Table 1). Most research was conducted in the northwest Atlantic (53.3%) and Mediterranean (33.3%) regions; this geographic bias led to the species bias, as loggerhead and green turtles predominantly nest in these regions. Only one study, in the southwest Indian Ocean (Dalleau *et al*., 2012), examined the impacts of climate change on nesting phenology in the Indian Ocean basin and no studies from Southeast Asia were found. The geographic and species bias indicates a knowledge gap in understanding the potential for climate change-driven changes in sea turtle nesting phenology in the Indian Ocean region, especially as sea turtles in the northwest Indian Ocean experience extreme nesting and foraging environments (e.g., Pilcher *et al*., 2014; Marshall *et al*., 2020; Chatting *et al*., 2021), key foraging grounds in Southeast Asia seas are threatened by marine heatwaves (Konsta *et al*., 2022), and other regional management units for species in the region are at risk from the threat of climate change or insufficient data is publicly available to predict the risk (Wallace *et al*., 2011). The knowledge gap can also be the result of challenges in collecting data, especially over a long time period, and the scarcity of baseline data for comparison.

Table 1. Sea turtle species and geographic region in studies (n=15) assessing the variation in nesting phenology with sea surface temperature. Totals exceed 100% as some studies examined more than one parameter.

Sea Turtle	% Studies	Region	% Studies
Loggerhead	73.3	Northwest Atlantic	53.3
Green	26.7	Mediterranean	33.3
Leatherback	6.7	East Pacific	6.7
		Southwest Atlantic	6.7
		Southwest Indian	6.7

Of the parameters of nesting ecology investigated, the most common were the start/onset and the length/duration of the nesting season (53.3% each), followed by the median day of the nesting season (46.7%; Table 2). Identifying the date on which the nesting season begins and ends, and calculating the median date, may require few resources and be potentially more accurate than ongoing monitoring of beaches throughout the nesting season to estimate peak nesting date, inter-nesting period, and start of hatchling emergence. Note that Patricio *et al*. (2021) suggests using the 2.5th percentile of the nesting date as a proxy for the commencement of nesting, to avoid any outlying data for populations with seasonal nesting. (The 2.5th percentile is the date before which 2.5% of nesting events occurred.) Researchers should also be aware that these metrics can be impractical for assessing shifts in nesting phenology in populations that have bimodal or year-round nesting (Dalleau *et al*., 2012).

Table 2. Parameter of nesting ecology examined in studies (n=15) assessing variation in nesting phenology with sea surface temperature. Totals exceed 100% as some studies examined more than one parameter.

Parameter Investigated	% Studies
Start/onset of nesting season	53.3
Length/duration of nesting season	53.3
Median day of nesting season	46.7
Peak nesting date	13.3
Length of inter-nesting period	6.7

SST data used in the studies we examined was primarily derived from central data sources (80.0%) at monthly intervals (50.0%) (Table 3). For instance, Pike *et al*. (2006) sourced their SST data from an automated data logger attached to buoy 41009 of the National Data Buoy Center. Similarly, Weishampel *et al*. (2004) obtained SST values from a National Oceanic and Atmospheric Administration (NOAA) buoy (Station 41009). Using environmental data from a central source removes the need for researchers to purchase and place data loggers at individual study sites. Future research could utilise satellite-derived SST data (see O'Carroll *et al*., 2019; Momin *et al*., 2022).

Table 3. Source, interval, and location of sea surface temperature data in studies (n=15) assessing the variation in nesting phenology with sea surface temperature.

Source	% Studies	Interval	% Studies	Location	% Studies
Central data source	80.0	≤60min	20.0	Nesting beach	60.0
Study data logger	20.0	6-12hr	6.7	Foraging grounds	26.7
		Daily	13.3	Both nesting and foraging habitat	13.3
		Weekly	6.7		
		Monthly	53.3		
		Annually	6.7		

Examining SST data from waters adjacent to nesting beaches alone was the most common approach (60.0%) (Table 3), potentially since nesting beaches are known locations and foraging areas for individuals in a nesting population may be broadly distributed geographically. Only two studies (13.3%) used SSTs at both foraging areas and nesting beaches to understand variation in nesting phenology with SSTs at different habitats. Their findings were different, but complementary. Loggerhead turtles in Brazil started their migration in response to environmental cues at foraging areas, which determines the onset of the nesting season (Mosinjon *et al*., 2019), whilst loggerhead turtles in Greece nested earlier after an increase in SST at the nesting site (Patel *et al*., 2016).

The majority of studies assessed potential changes in nesting phenology at only one nesting location (73.3%; Table 4). Data sets across all studies ranged from 1-36 years in length; studies at single locations examined data from a Mean±StDev duration of 16.6±7.3yr (range 4-26yr). This area of research would potentially benefit from broad acceptance of the standards for appropriate baseline data and temporal scale of data needed to determine changes in nesting phenology with appropriate statistical power.

Finally, we emphasise that comparison of findings among studies can be challenging (Patricio *et al*., 2021). The onset of nesting may reflect atypical events (outliers) and the median nesting date can also be ambiguous given that it is affected both by the onset and duration of the nesting season (Mazaris *et al*., 2013) as well as survey effort (Patricio *et al*., 2021). Changes in sea turtle nesting phenology parameters in response to SST has also been found to vary with latitude (Mazaris *et al*., 2013).

Table 4. Number of nesting sites in studies (n=15) assessing the variation in nesting phenology with sea surface temperature.

# Nesting Sites	% Studies
1	73.3
3	13.3
6	6.7
223	6.7

SUMMARY

Sea turtle populations in the Indian Ocean and southeast Asia are threatened by climate change, and some are data deficient on the potential impacts of this threat (see Phillott & Rees, 2021). We have summarised the methods used in worldwide studies that assessed changes in nesting phenology with climate change published from 2000-2021 to inform researchers interested in similar studies at their nesting and/or monitoring sites. Our summary does not imply that the same method(s) would be the most suitable for all locations, but the information we present can be used as a starting point for researchers new to the field of study. We also remind researchers to be cautious and not to assume climate change-induced changes in sea turtle nesting phenology, since reproductive ecology depends on many factors, including resource availability and acquisition, environmental cues at foraging and breeding sites, courtship, population demographics, and geography (Patricio *et al*., 2021).

ACKNOWLEDGEMENTS

We acknowledge the suggestions from the anonymous peer-reviewers, which were incorporated into the paper.

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