OLIVIA GARCIA

VARIABILITY IN THE EFFECT OF CLIMATE VARIABLES ON THE REPRODUCTIVE OUTPUTS OF SEA TURTLES THAT SHARE NESTING GROUNDS

UNIVERSIDADE DO ALGARVE

Faculdade de ciências e tecnologia

2024

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Mestrado em Biologia Marinha

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Declaro ser a autora deste trabalho, que é original e inédito. Autores e trabalhos consultados estão devidamente citados no texto e constam da listagem de referências incluída.

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I declare I am the author of this work, which is original and unpublished. The sources consulted have been duly cited in the text and included in the list of references.

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ACKNOWLEDGMENTS OF THE THESIS

My heartfelt thanks to Dr Mariana Fuentes for agreeing to supervise this thesis and her role as a liaison with Projeto Tamar. Despite the geographical distance and time difference, Dr Fuentes has been an incredibly reliable and dedicated supervisor and an invaluable mentor in this process of learning the ins and out of data analysis and scientific writing.

I am grateful to the entire Projeto Tamar team in Brazil for their dedication and contribution to marine turtle conservation and awareness. Their efforts in supporting data collection, scientific research and public education are truly invaluable.

My appreciation goes to Professor Rita Castilho for kindly agreeing to serve as my internal supervisor and offering her expert advice and insights into the academic world.

I wish to thank my dear friend and housemate Antonia Mallman for her support, advice and constructive feedback on some of my drafts. I am so grateful to Eve-Marine Pubert, Clément Esclavy, Emilia Kotiranta and Melina Kalanzis for being the greatest friends ever and for their never-ending solidarity throughout the whole master’s program.

Finally, I feel the deepest gratitude to my family for their emotional and financial support throughout my long studies, always encouraging me to pursue the degree of my choice in the location of my choice and making sure I always felt supported throughout the process. I am very fortunate to have you and am forever grateful to you all.

ABSTRACT

Climate change is expected to impact animals whose life history traits are reliant on environmental parameters. This is the case for sea turtles, who lay their eggs at temperate and tropical beaches and have the development of their embryos dependent on environmental conditions at their nesting grounds. Understanding how sea turtles reproduction will be impacted by climate change is crucial to guide effective management and help maintaining sea turtle populations. Studies that have explored the effects of local climate variables on sea turtles reproductive outputs have focused on individual species, with no research to date comparing effects across species that nest at the same location and under similar conditions. We address this knowledge gap by comparing the effects of climate variables on nests from different species at shared nesting grounds. We used Generalized Additive Models (GAMs) to explore how air temperature, sand temperature, precipitation and humidity affect reproductive outputs of *in situ* nests of loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea),* hawksbill (*Eretmochelys imbricata*) and olive ridley (*Lepidochelys olivacea*) sea turtles. Our results show variability in the response of species that nest at the same location with the same seasonality. We conclude that embryos response to local climate is also species specific and therefore, conservation efforts at nesting grounds should take into consideration not only the conditions at each site but also the requirements of each species.

Key words: sea turtles, climate change, hatching success, emergence rate, reproductive outputs, scientific modeling

RESUMO

As alterações climáticas, provocadas pelas emissões de gases com efeito de estufa induzidas pelo homem, estão a perturbar significativamente os sistemas climáticos da Terra e a manifestar-se através do aumento das temperaturas globais e da alteração dos padrões meteorológicos. Prevê-se que estas alterações afectem todos os ecossistemas, sendo particularmente vulneráveis as espécies cujos ciclos de vida e desenvolvimento estão diretamente ligados às condições ambientais. As várias regiões e ecossistemas do mundo sofrem diferentes níveis de impacte. Na maioria das regiões, as alterações climáticas traduzem-se em alterações das temperaturas ou dos padrões de precipitação e dos ciclos hidrológicos. Estas perturbações são alarmantes, uma vez que aumentam a frequência de fenómenos meteorológicos extremos, secas prolongadas, aceleram o recuo dos glaciares e a desertificação. Em consequência, muitas espécies estão ameaçadas nos seus habitats históricos, com algumas delas a deslocarem as suas áreas de distribuição tradicionais e a migrarem em direção aos pólos, à medida que seguem condições ambientais mais adequadas ao seu metabolismo, aos seus hábitos de alimentação ou de acasalamento. Quando as condições ambientais se tornam desfavoráveis, estes organismos passam a estar em condições metabólicas sub óptimas. Dada a sua dependência dos parâmetros ambientais e a sua limitada capacidade de adaptação em tempo real, prevê-se que os organismos ectotérmicos sejam particularmente afectados pelas alterações climáticas.

As tartarugas marinhas são importantes ectotérmicas marinhas que desempenham papéis importantes tanto nos seus locais de alimentação como de reprodução. Estão particularmente em risco com as alterações climáticas, uma vez que os seus processos reprodutivos dependem das condições ambientais nos seus locais de nidificação. Depositam os seus ovos em praias temperadas e tropicais e o sexo das crias é determinado pela temperatura da areia durante o parte da incubação: temperaturas mais elevadas produzem fêmeas, enquanto temperaturas mais baixas produzem machos. Os ovos devem ser incubados num intervalo de temperatura estreito (~25°C a 35°C), fora do qual os embriões não se desenvolvem e o sucesso da eclosão diminui significativamente. A temperatura também afecta a aptidão e a qualidade

da incubação e outros factores, como a precipitação e os níveis de humidade, afectam as taxas de eclosão ou a capacidade de os recém-nascidos emergirem dos ninhos.

Dada a sua dependência dos parâmetros ambientais, todas as espécies de tartarugas marinhas serão direta e indiretamente afectadas pelas alterações climáticas, com impactos que variam em termos geográficos, temporais e entre espécies e populações. Embora as tartarugas marinhas tenham demonstrado alguma capacidade de adaptação às flutuações ambientais, é provável que o ritmo acelerado das actuais alterações climáticas ultrapasse a sua capacidade de contrariar essas alterações e ameace a viabilidade das suas populações. Os esforços de conservação nos locais de nidificação estão a implementar estratégias como o sombreamento, a rega ou a relocalização dos ninhos, numa tentativa de proporcionar condições óptimas para os ninhos e atenuar os efeitos das variações climáticas nas praias onde as condições climáticas estão a mudar. Para orientar uma gestão eficaz e precisa das praias de nidificação, é crucial compreender o efeito das variações climáticas nas diferentes espécies de tartarugas marinhas e adaptar a gestão às especificidades de cada zona de nidificação.

As investigações realizadas até à data que exploraram os efeitos das variações climáticas nos ninhos in situ encontraram variabilidade entre espécies e locais, mas os trabalhos centraram-se sempre numa única espécie. Por conseguinte, ainda não é claro se todas as diferentes espécies de tartarugas marinhas reagem de forma diferente a variações no seu ambiente local ou se esta variabilidade pode ser atribuída às diferentes condições climáticas registadas nos locais estudados. Para reduzir esta lacuna de conhecimento, esta tese propõe expandir a investigação anterior e explorar a forma como as variações no clima local afectam os ninhos de espécies que partilham o mesmo local de nidificação. Uma hipótese é que as respostas dos embriões são semelhantes em todas as espécies e que os efeitos do clima local dependem principalmente das caraterísticas do local onde os ovos são postos. A segunda hipótese é que as respostas são também específicas de cada espécie e que este facto deve ser tido em conta na implementação da gestão dos locais de nidificação.

Utilizamos dados históricos de ninhos de tartarugas marinhas coletados entre 2013 e 2020 pela Fundação Projeto Tamar, o instituto Brasileiro de conservação marinha, em três

importantes praias de nidificação, de quatro espécies diferentes de tartarugas marinhas:a tartaruga cabeçuda (*Caretta caretta),* a tartaruga-de-couro (*Dermochelys coriacea*), a tartaruga-de-pente (*Eretmochelys imbricata*) e a tartaruga-oliva (*Lepidochelys olivacea).* Os dados consistem em coordenadas geográficas, data de postura, data de eclosão, número de ovos eclodidos e não eclodidos por ninho e número de ovos eclodidos que emergiram dos ninhos. A partir desses dados foi possível determinar o sucesso da eclosão e as taxas de emergência para cada ninho. Apenas os ninhos com dados climáticos locais disponíveis de forma consistente antes e durante toda a incubação foram incluídos no estudo. Também não foram incluídos ninhos que sofreram predação ou afectados por tempestades. Obtivemos dados climáticos locais (temperatura e humidade do ar e precipitação) das estações meteorológicas costeiras mais próximas, fornecidos pelo site do Instituto Nacional de Meteorologia (INMET). As temperaturas da areia foram obtidas a partir de *data loggers* instalados nos locais de estudo. Foram usados testes não-paramétricos para comparar os resultados entre espécies e locais e Modelos Aditivos Generalizados (GAMs) para examinar a influência das variáveis climáticas nos resultados obtidos em diferentes escalas temporais, até dois meses antes da postura dos ovos até à data de eclosão.

Encontrámos uma variabilidade significativa nos resultados entre locais dentro da mesma espécie e entre espécies que partilham o mesmo local com a mesma sazonalidade e clima semelhante. Isto indica que a resposta dos embriões é também específica por espécie e que este facto deve ser tido em conta quando se implementam estratégias de conservação e gestão nos locais de desova. Todos os quatro preditores climáticos locais (temperatura e humidade do ar, precipitação e temperatura da areia) tiveram uma influência significativa e cumulativa nos ninhos, mas o ajuste dos GAMs diminuiu com tamanhos de amostra maiores, sugerindo que outros parâmetros não incluídos no estudo influenciam significativamente este tipo de resultados. Dada a variabilidade dos nossos resultados, esperamos que as quatro espécies de tartarugas marinhas sejam afectadas de forma diferente pelas projecções de alterações climáticas. Neste contexto, é crucial uma compreensão sólida de tais interações para desenvolver intervenções de conservação adequadas e mitigar os efeitos que a mudança dos padrões climáticos terá sobre as espécies que dependem de parâmetros ambientais. Este estudo visa contribuir para uma base de informação que ajudará a prever impactos futuros e a orientar a gestão de importantes áreas de nidificação de tartarugas marinhas.

Palavras-chave: tartarugas marinhas, alterações climáticas, sucesso de eclosão, taxa de emergência, resultados reprodutivos, modelização.

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LIST OF ABBREVIATIONS

AIC. Akaike Information Criterion
CC. *Caretta caretta* (Loggerhead sea turtle)
DC. *Dermochelys coriacea* (Leatherback sea turtles)
edf. Effective degrees of freedom
EI. *Eretmochelys imbricata* (Hawksbill sea turtle)
ER. Emergence rate
ENSO. El Niño Southern Oscillation
GAM. Generalized Additive Model
GLMER. Generalize Mixed Linear Model
HS. Hatching success
INMET. Instituto Nacional de Meteorologia
IPCC. Intergovernmental Panel on Climate Change
IUCN. International Union for Conservation of Nature
IUCN-SSC. International Union for Conservation of Nature – Species Survival Commission
LO. *Lepidochelys olivacea* (Olive Ridley sea turtle)
P. p_value
R^2. R-squared
REML. Restricted Maximum Likelihood
RMU. Regional Management Unit
SWOT. State of the World's Sea Turtles
TCP. Thermal performance curve
TSD. Temperature-dependent sex determination
TSP. Thermosensitive period
VUE. Vemco User Environment

GENERAL INTRODUCTION

1. Climate change is impacting ectotherms

1.1.Climate change

Anthropogenic climate change, driven by excessive human emissions of greenhouse gases, is causing significant alterations to the Earth energy balance and climate system (IPCC, 2021). The release of greenhouse gases enhances the natural greenhouse effect of the Earth, trapping more of the sun's heat into the atmosphere and leading to global warming. Warming is not homogenous and habitats worldwide are affected differently; local effects may not extend regionally, regional effects can vary, and not all regions experience warming at the same rate (Burrows et al., 2011). The impacts go beyond temperature changes, with some areas seeing shifts in precipitation patterns or more extreme weather events. Marine ecosystems are also affected, as increasing carbon dioxide levels alter basic oceanic properties (e.g. acidification of ocean waters) and coastal habitats are being modified with sea level rise, following the temperature-induced expansion of the ocean (Feagin et al., 2005; Guinotte & Fabry, 2008; Trenberth, 2011; Church et al., 2011).

Different ecosystems do not experience the same level of impact from climate change (Burrows et al., 2011). In temperate regions, alterations in precipitation patterns can lead to more frequent extreme weather events, such as heavy rainfall and flooding, as well as prolonged droughts (Trenberth, 2011). In arid and semi-arid regions, climate change worsens water scarcity and accelerates desertification (Hillel & Rosenzweig, 2002; Huang et al., 2020). Mountainous regions face impacts like melting glaciers, altered hydrological cycles, and higher risks of landslides and avalanches (Kundzewicz, 2008; Roe et al., 2017). In polar regions, rapid warming causes sea ice loss, glacier melt, permafrost thawing, and ecosystem changes (Robinson, 2022). Biodiversity is affected across all regions, with species shifting their geographic ranges poleward as they follow temperature that are more suited to their foraging or mating habits (Mancino et al., 2022; Mason et al., 2015).

1.2. Ectotherms

Ectotherms (also known as cold-blooded organisms) are animals whose body temperature is primarily determined by their external environment rather than internal physiological processes (Wieser, 1973). They represent the majority of animal species, including most invertebrates (e.g. insects, arachnids, crustaceans), most fish species (excepted some species of tuna and shark), reptiles (e.g. snakes, lizards, turtles and tortoises), and amphibians (e.g. frogs, toads, salamanders). They populate a vast range of habitats, from the deep sea to almost every terrestrial environment. Unlike endotherms (warm-blooded animals), which regulate their body temperature through internal metabolic processes, ectotherms rely on external heat sources to manage their body temperature (Dreisig, 1984). Without the adequate external temperature, the physiological processes responsible for important functions in ectotherms may not be sustained (Huey & Stevenson, 1979; Witherington & Ehrhart, 1989; Mondal & Rai, 2001; Schulte, 2015).

To regulate their body temperature, ectotherms adapt their activity based on the time of the day and use specific behaviors such as sunbathing to warm up, or shade seeking and burrowing to cool down (Dreisig, 1984; (Black et al., 2019). Physiological adjustments involving changes in enzyme activities, membrane fluidity, and metabolic pathways to optimize cellular functions help them cope with environmental variations (Huey & Bennett, 1990; Pörtner et al., 2007; (Žagar et al., 2018). While most ectotherms primarily rely on external heat sources, some can also produce heat through metabolic processes like digestion and muscle contraction (Angilletta et al., 2002). Extreme temperatures can be lethal (Nguyen et al., 2011) as each ectothermic organism possess a critical thermal minimum and a critical thermal maximum, or the lowest and highest temperatures at which they can function. Ectothermic organisms can recover from brief exposures to critical temperatures if they return to their optimal temperature range, with a recovery depending on the duration and severity of the thermal stress (Hutchison & Maness, 1979). If exposure is prolonged, metabolic disruptions and impaired enzyme functions happening can ultimately lead to death (Nguyen et al., 2011).

Almost all aspects of the behavior and physiology of ectotherms are sensitive to their body temperature, including their feeding and growth rates (Kingsolver & Woods, 1997), locomotion (Ojanguren & Brañta, 2000), foraging abilities (Fukuoka et al., 2022), immune responses (Mondal & Rai, 2001) and courtship behaviors (Navas & Bevier, 2001). Optimal performance typically occurs within a specific temperature range, known as the thermal performance curve (TCP, Huey & Kingsolver, 1989). The bell-shaped curve is characterized by an optimal temperature (Topt), at which the organism's performance is maximized, and a thermal breadth, or a range between temperatures where performance is at about 50% of its maximum. Chronic exposure to temperature near critical limits have an impact on basic behaviors such as foraging, mating, or predator avoidance and can ultimately impact a whole population (Gunderson et al., 2017).

Given their reliance on external temperature, ectotherms are particularly dependent on environmental conditions at their habitats. Thus, they are expected to be especially vulnerable to consequences from climate change, with possible impacts including alterations to their behavior, fitness and body size, decreased reproductive success, and shifts in the distribution of their habitats. (Martinez et al., 2016; Hayden Bofill & Blom, 2024).

1.3. Effects of climate change on the physiology and ecology of ectotherms

Since ectotherm's basic physiological functions are strongly dependent on environmental temperatures, they are generally more susceptible to variations in local climate (Rohr & Palmer, 2013). Climate warming consequences observed on ectotherms manifest in various physiological and ecological changes. Declines in ectotherms body size have been linked to climate warming, resulting from higher developmental temperatures which accelerate growth rates by shortening development periods but lead to smaller adult sizes (Ohlberger, 2013; Martinez et al., 2016). Rising temperatures increase metabolic rates in ectotherms, which elevates energy demands and can lead to greater food intake requirements, increased foraging activity, and higher vulnerability to predators and other environmental stresses (Dillon et al., 2010). Increased metabolic activity may accelerate physiological processes, leading to oxidative damage and potentially shorter lifespans and faster aging (Bestion et al., 2015; Burraco et al., 2020). Significant temperature variations can also alter levels of fitness in ectotherms (Paaijmans et al., 2013).

The impacts of anthropogenic climate change on terrestrial organisms are often predicted to increase with latitude, since higher latitudes tend to experience a greater magnitude of warming (IPCC, 2014). Kingsolver et al. (2013) modeled the impacts of heat stress and its fitness consequence for terrestrial ectotherms and suggests that mid-latitude species will be particularly susceptible to heat stress associated with climate change due to temperature variation. However, when modelling the effects of anthropogenic climate change on four major group of ectotherms (insects, turtles, lizards and frogs), Deutsch (2008) found the impacts of anthropogenic climate change to be greater at low latitudes (tropics) for all groups. The study illustrate that tropical ectotherms are particularly vulnerable due to their narrow thermal tolerances, with warming temperatures pushing many species closer to their thermal maxima, leading to potential population declines. Thus, the biological impact of rising temperatures is highly dependent on the physiological sensitivity of organisms to temperature changes.

Climate change also impacts the geographic distribution and population dynamics of ectotherms. As global temperatures rise, some species migrate to more suitable habitats to maintain their physiological functions. This often results in shifts toward higher latitudes or elevations where the climate remains within their optimal thermal range (Parmesan, 2006; Mancino et al., 2022).

1.4. Effects on ectotherms reproduction

Changes in climate, particularly temperature and precipitation, can have profound impacts on ectotherms reproductive processes, affecting everything from mating behavior to reproductive onset and the viability of offspring (Gibbs & Breisch, 2001; Matsuzawa et al., 2002; Chadwick et al., 2006; Bestion et al., 2015). Their reproduction is intricately linked to their environment since they exhibit a range of reproductive strategies that are heavily influenced by temperature. In species with temperature dependent sex-determination (TSD), where the temperature at which embryos incubate determines the sex of offsprings, even slight increases in temperature can skew sex ratios, potentially leading to population declines if one sex becomes disproportionately represented (Schwanz & Janzen, 2008). Furthermore, ectotherms' reproductive cycles are often synchronized with seasonal temperature patterns. Higher temperatures can alter the timing of reproduction, with potential mismatches between life cycle events and environmental conditions or between the two sexes of a same species (Beebee, 1995; Blaustein et al., 2001; Chadwick et al., 2006). Warmer temperatures can accelerate development and shorten the time required for eggs to hatch or larvae to metamorphose into adults. This rapid development can come at a cost, as it may reduce the overall fitness and survival of the offspring in some species (Matsuzawa et al., 2002; Booth et al., 2004).

For amphibians and reptiles that rely on coastal areas as nurseries (sand banks, intertidal pools), sea level rise poses a significant challenge by modifying the coastline, erasing historical breeding sites and forcing animals to relocate (Pike et al., 2015; Von Holle et al., 2019; Rivas et al., 2023). For many species, precipitation is an important factor for egg deposition and spawning activity. Climate-induced changes in temperatures and precipitation patterns can alter the quality of breeding sites, lead to the desiccation of eggs or flooding of nests, which can severely impact reproductive success (McGehee, 1990; Mills & Barnhart, 1999; Limpus et al., 2021). Unusual increases in rainfall and humidity also create favorable conditions for pathogens and parasites, further reducing the survival rates of offspring (Bézy et al., 2015).

1.5 Adaptations and acclimation

Ectotherms are capable of important genetic, physiological and behavioral adaptations to mitigate the effects of temperature variations (Ortega et al., 2016). Organisms submitted to exposure to temperatures that approach their thermal limits have demonstrated shifts in their physiological performance curves and expansions of their thermal tolerance (Hutchison & Maness, 1979; Huey & Kingsolver, 1989). Phenotypic plasticity plays an important role in in ectotherm in response to increasing mean temperatures, by allowing gene expression modification in response to temperature variations (Logan & Cox, 2020). Additionally, behavioral acclimation is common with most organisms adapting their daily activities to temperature variations and others actively seeking new habitats or nurseries that offer optimal thermal conditions (Dubois et al., 2009; Mancino et al., 2022).

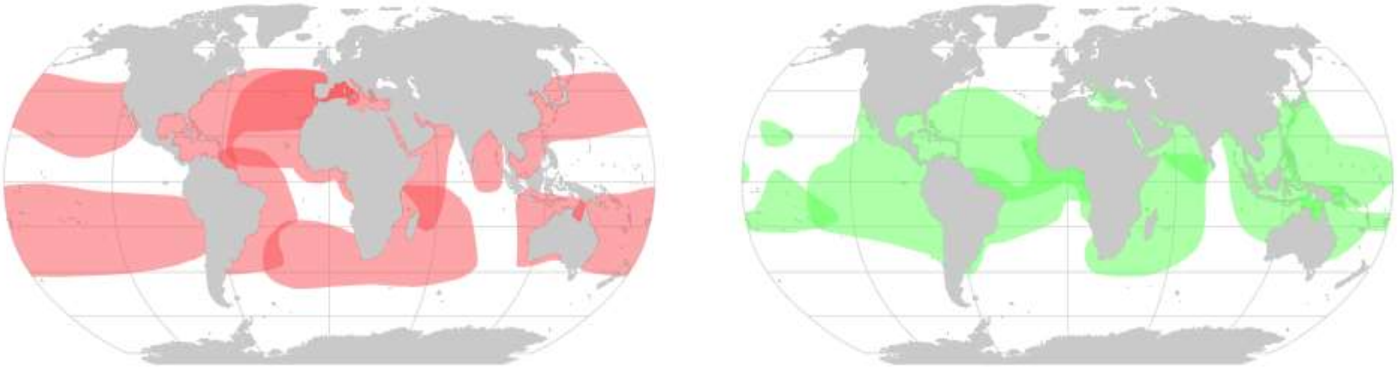
Such capacities are not universal and acclimation abilities not uniform between species and locations (Angilletta et al., 2002; Calosi et al., 2013; Rohr et al., 2018; Morley et al., 2019).

While some species subjected to temperatures higher than their annual average have shown full acclimation (Donelson et al., 2012), other studies found other species to fail to adapt after being exposed extensively to temperatures just a few degrees above their annual average (Peck et al., 2010). Even species with high acclimation capacities face limits and rapid or extreme climatic changes can outpace the ability of species to adapt (Somero, 2010; Morley et al., 2019; Logan & Cox, 2020). Ultimately, organisms with the greatest risk from rapid climate change are those with a low tolerance for warming, limited acclimation ability, and reduced dispersal (Meyers & Bull, 2002).

2. Sea turtles

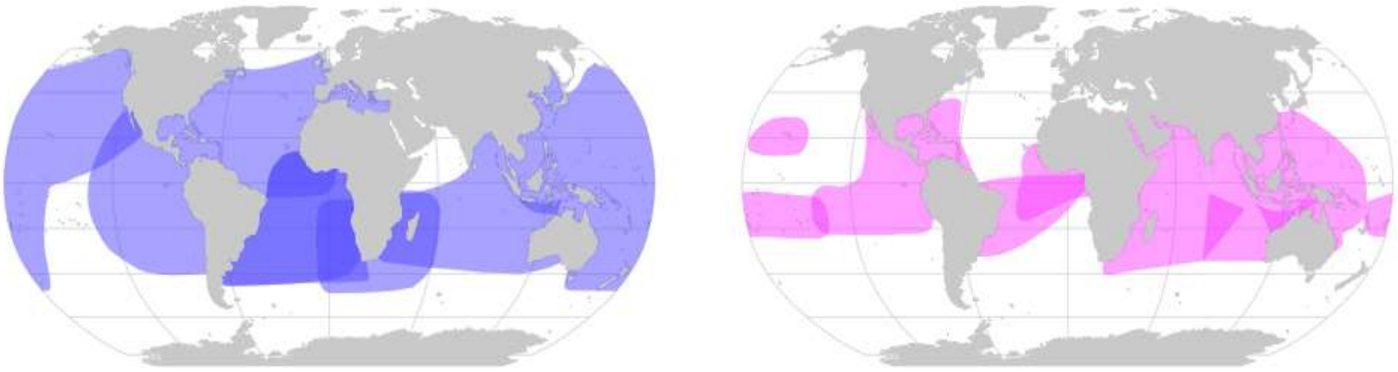
2.1 An important marine ectotherm

Sea turtles, also known as marine turtles, are large marine reptiles inhabiting most tropical and subtropical regions of the ocean (Wallace et al., 2023). They comprise seven species categorized into two families: Cheloniidae and Dermochelyidae. The Cheloniidae family includes the green turtle (*Chelonia mydas)*, loggerhead turtle (*Caretta caretta*), hawksbill turtle (*Eretmochelys imbricata*), olive ridley turtle (*Lepidochelys olivacea*), the Kemp's ridley (*Lepidochelys kempii*) turtle and the flatback sea turtle (*Natator depressus*). The Dermochelyidae family is represented by a single species, the leatherback turtle (*Dermochelys coriacea*), differing from other sea turtles species with its larger size, distinct shell structure and physiological regulation capacities that allow it to inhabit colder waters (Davenport, 1997; Casey et al., 2014). Since sea turtles are ectotherms, their body temperature and metabolic rates depend on the surrounding environmental temperatures, which also influence crucial aspects of their life-history traits such as egg incubation and sex determination of their offspring (Davenport, 1997) They typically forage and nest in tropical and temperate seas but are not found in high latitudes, where the colder waters don't suit their physiology. Their diet varies widely by species or age, ranging from carnivorous and herbivorous to gelatinivorous (feeding on soft zooplankton like jellyfish and other invertebrates) or transitioning from primarily carnivorous in juvenile stages to an herbivorous diet in adulthood (K. A. Bjorndal, 1985).



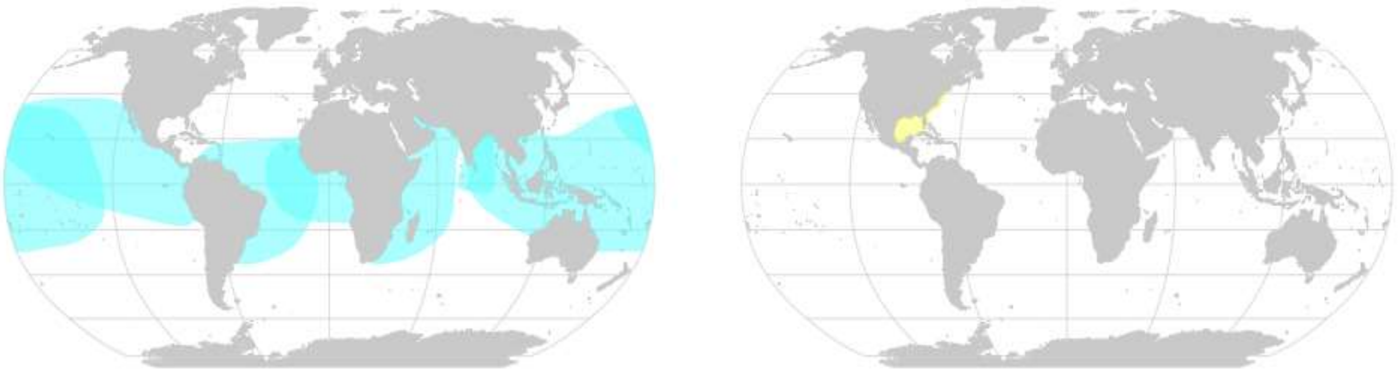
Loggerhead turtle *(Caretta caretta)*

Green turtle *(Chelonia mydas)*



Leatherback turtle *(Dermochelys coriacea)*

Hawksbill turtle *(Eretmochelys imbricata)*



Olive ridley turtle *(Lepidochelys olivacea)*

Kemp's ridley turtle *(Lepidochelys kempii)*

Figure 2.1 : Global distribution of sea turtles regional management units (RMUs). Data source: State of the World's Sea Turtles (SWOT) report 2023, after Wallace et al., 2023. *Note*. The flatback sea turtle (*Natator depressus*) RMUs are not represented due to insufficient data available.

Sea turtles serve important roles at both their nesting and foraging habitats. Green and hawksbill sea turtles, for instance, contribute to the maintenance of important marine ecosystems such as coral reefs and seagrass meadows by feeding off competitive species (Meylan, 1988; Goatley et al., 2012). Loggerhead, green and especially leatherback sea turtles regulate jellyfish populations that would otherwise proliferate and negatively impact fish stocks by preying on fish larvae and eggs (Sommer et al., 2002; Lynam et al., 2006). The activity of sea turtles grazing has beneficial effects on seagrass beds, by renewing seagrass blades, enhancing their nutrient content and tolerance to eutrophication (Moran & Bjorndal, 2007; Christianen et al., 2012). Fast growing sponges that compete with coral for space are consumed by the hawksbill turtles inhabiting the reefs (A. Meylan, 1988). At their nesting grounds, sea turtles influence community dynamics by providing nutrients to the ecosystem in the form of their unhatched eggs, of which benefit both beach predators and dune vegetation (Bouchard & Bjorndal, 2000). All species migrate great distances, connecting different marine ecosystems and facilitating the transfer of nutrients across distant habitats (Bouchard & Bjorndal, 2000). Additionally, their presence adds value to the tourism industry (Hendrix & Pérez-Espona, 2024).

Most sea turtle species are listed as Vulnerable, Endangered or Critically Endangered on the IUCN Red List (IUCN-SSC, 2023). The majority of threats they are facing are of anthropogenic nature and include climate change, habitat loss along coastlines, pollution, fisheries bycatch and direct take. Their migratory nature and use of a variety of habitats (terrestrial, benthic, neritic or epipelagic) complicate research efforts and call for a comprehensive, multidimensional approach to fully understand the effects of all the different stressors throughout different life stages. The interaction between stressors is complex and their effects may be synergistic or cumulative (Fuentes et al., 2023). To facilitate conservations strategies, sea turtle populations have been organized into Regional Management Units (RMU) to spatially define and identify populations segments within species (Wallace et al., 2010; Wallace et al., 2023). These units often span multiple countries and even continents. Thus, there is a need for international cooperation in conservation efforts; such efforts are still variable around the world. Although some populations are showing signs of recovery due to rigorous protection measures, others show no evidence of recovery or continue to decline (Mazaris et al., 2017; Hendrix & Pérez-Espona, 2024).

2.2 Reproduction

Sea turtles are oviparous and lay eggs in sandy beaches at tropical or subtropical grounds. Some nesting grounds are renowned for being used by several species almost all year round, while others only occasionally host nests. Sea turtles are long-lived animals that have a late sexual maturity, with variability between species. While most species of sea turtles can take two to three decades to reach sexual maturity (Casale et al., 2011; Turner Tomaszewicz et al., 2022), estimations on green sea turtles range from 16 up to 40 years old (Limpus & Chaloupka, 1997). Sea turtles reproduction unfolds in several stages. Females migrate long distances from their foraging grounds to nesting grounds, often traveling back to regions where they were born. It is thought that they navigate by sensing the Earth's magnetic field and imprint on the magnetic and chemical signatures of their natal beaches (Meylan et al., 1990; Lohmann & Lohmann, 1994; Nordmoe et al., 2004). Mating usually occurs offshore, often near the nesting beaches (James et al., 2005). Females lay multiple nests in one season, resting at sea between lays and coming ashore only to lay their eggs (Walcott et al., 2012; Hart et al., 2019).

Nesting typically happens at night to avoid predators and heat stress. Females dig body pits and egg chambers where they deposit eggs. The number of eggs per nest varies by species, with green and loggerhead turtles laying about 100-150 eggs while leatherbacks lay around 80-100 eggs (Hays & Speakman, 1992; Hays et al., 1993; Reina et al., 2002). Incubation temperature influences both the incubation period (typically 45-75 days) and sex of the hatchlings through temperature-dependent sex determination (TSD), with warmer temperatures producing more females (Mrosovsky, 1980). Hatchlings emerge mostly at night and independently make their way to the ocean, where many of them fall prey to predators and only a slim percentage reaches the open ocean and adulthood.

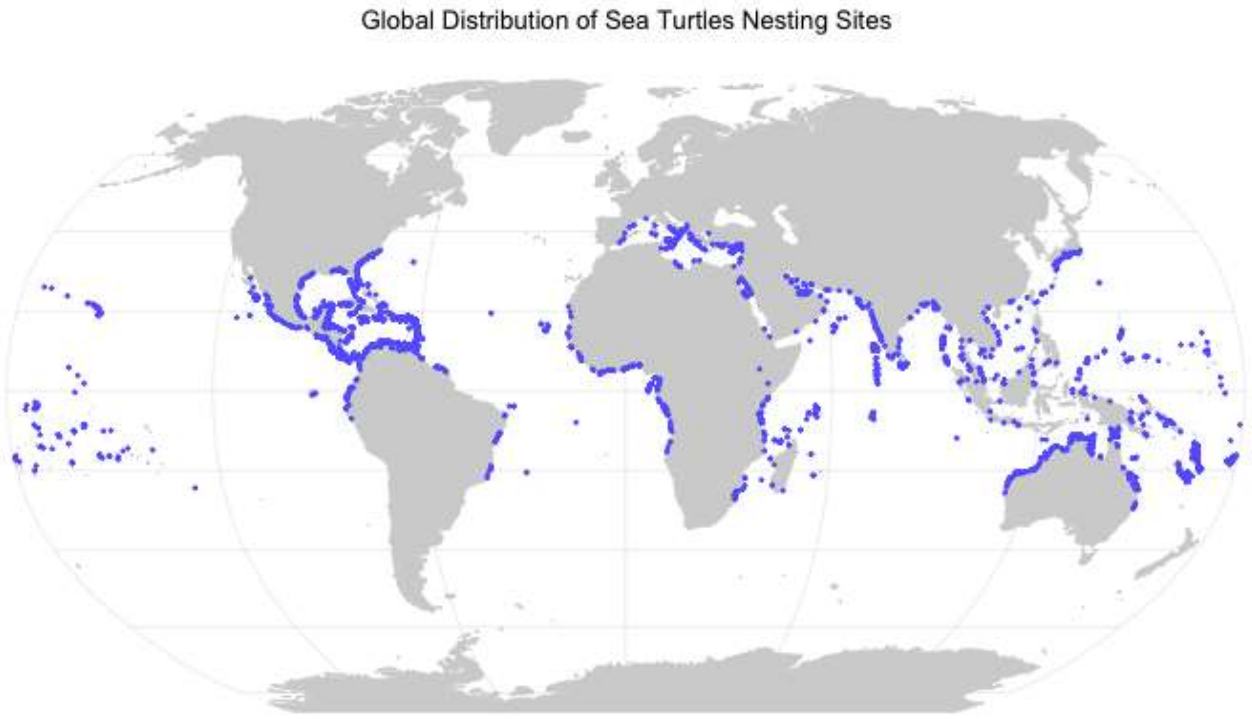


Figure 2.2 : Global distribution of sea turtles nesting sites. Data source: State of the World's sea turtles (SWOT) report, 2023.

2.3. Temperature-dependent sex determination

A variety of sex determination systems are identified amongst the animal kingdom (Li & Gui, 2018; Cook, 2002). In most animal species, sex is determined chromosomally, and embryos have their gender determined during fertilization by genetic factors alone. For other species, sex chromosomes are not present and sex determination is environmental: the gender of the embryo depends on environmental factors that act after fertilization of the eggs. Sea turtles and other ectothermic species have temperature-dependent sex determination (Bull, 1980), where the sex of the developing embryos is determined by the temperature at which the eggs are exposed during their development (Yntema & N. Mrosovsky, 1980).

TSD exists in different patterns, classified based on how temperature influences sex ratios. In Type I TSD, found in sea turtles and most TSD species, either a higher proportion of one sex is produced at higher temperatures and the other sex is produced at lower temperatures. The TSD thermal response curve is defined by a pivotal temperature, at which an equal number of embryos within a clutch develop as males and females, and a transitional range or the range of temperatures under which either male or female offspring will be produced (Mrosovsky & Pieau, 1991). In sea turtles, higher temperatures produce more females in the nests.

TSD occurs during the thermosensitive period (TSP) of embryonic development, often located around the embryos mid-development (Yntema & N. Mrosovsky, 1980, Merchant-Larios et al., 1997). During the TSP, the ambient temperature influences the activity of genes and enzymes involved in the sexual differentiation process. The main molecular actor in TSD is the aromatase enzyme, which converts androgens, the group of hormones primarily responsible for the development of male characteristics in organisms, into estrogens, responsible for the development of female functions. In turtles, higher incubation temperatures enhance the activity of aromatase, leading to increased estrogen production and a higher likelihood of female development (Crews & Bergeron, 1994). On the contrary, lower temperatures reduce aromatase activity and favor male differentiation (Dorizzi et al., 1994).

3. Local climate variations impact sea turtles reproduction

3.1 Sea turtle nests are dependant on conditions at nesting grounds

Attention to sea turtle conservation needs was brought by early observations of herpetologist and conservationist Archie Carr during the mid-twentieth century, highlighting for the first time the importance of nesting sites. Mrosovsky and Yntema (1980) brought the first evidence of sea turtles dependence to temperatures by describing for the first time TSD in loggerhead sea turtles and establishing that successful egg incubation only occurred between 26-34°C. They found temperature to influence incubation duration and identified the middle third of incubation as critical for sea turtles sex determination. Further studies on other sea turtle species identified pivotal temperatures (at which both male and females hatchling were equally produced) and modelled transitional TSD ranges (Miller & Limpus, 1981; Morreale et al., 1982; (Ruiz et al., 1981)).

Their work raised the first concerns about the effects of rising temperatures on sea turtles primary sex ratios and predicted a feminization of populations following climate change projections (Mrosovsky & Yntema, 1980). This topic has since generated considerable volume of research (Reneker & Kamel, 2016; Jensen et al., 2018; Santidrián Tomillo & Spotila, 2020; Maurer et al., 2021) and it is now understood that temperature has effects beyond sex determination : it also affects embryonic development, hatchling size and fitness, locomotion, and overall hatchling viability (Booth & Astill, 2001; Matsuzawa et al., 2002; Booth et al., 2004; Booth, 2017). Factors like precipitation or moisture, initially studied as parameters influencing nest temperature (Lolavar & Wyneken, 2015), were eventually found to also directly affect fitness and quality of sea turtles hatchlings (Mc Gehee, 1990, Erb et al., 2018 Gatto & Reina, 2020; Matthews et al., 2021) as well as hatching rates within the nests and ability of hatchling to emerge from nests (Rivas et al., 2018). These findings implies that the resilience of turtle populations is highly dependent on the stability of local climate features at their nesting grounds. Punctual climate events, interannual variations or unfavorable environmental factors would challenge a whole population by providing fewer recruits in a specific nesting season.

3.2 Conservation and mitigation strategies at nesting grounds

Although sea turtles have shown some ability to adapt to variations in their environment, such as shifting their nesting season to more favorable times of the year (phenological shift; Weishampel et al., 2004) or shifting their range to more suitable areas (Pike, 2013; Fuentes et al., 2020; Mancino et al., 2022) the rapid pace of current climate change is likely to outpace their capacity to counteract these changes (Fuentes et al., 2024). Conservation efforts have thus developed strategies to mitigate the impacts of climate change on specific nesting grounds and vulnerable populations, aiming to maintain balanced sex-ratios and enhance reproductive success.

Strategies like relocation, shading and watering of nests are commonly used at nesting grounds. Relocating nests to safer locations or protected hatcheries help avoid predation, flooding, or destruction by weather events. Relocation is also effective at influencing incubation temperatures to balance sex ratios at grounds were sand temperatures exceed pivotal thresholds, but may reduce hatching success within nests (Pintus et al., 2009). Shading of nests has proven to be an effective methods for managing nest temperatures without compromising fitness or hatching success (Patino-Martinez et al., 2012; Hill et al., 2015; Staines et al., 2019). In the Lesser Antilles, shading techniques using palm tree leaves significantly reduced the proportion of female hatchlings in nests from an area with extreme female-biased sex ratios (Esteban et al., 2018). Irrigation of nests is an alternative strategy to manage nest temperature. Watering can lower sand temperatures and increase hatching success in excessively hot or dry areas (Lolavar & Wyneken, 2021). While temperature effects dissipate rapidly, moisture content changes are more lasting, thus beneficial for areas with low rainfall (Hill et al., 2015). However, irrigation must be used cautiously, as multiple factors, including ambient conditions, substrate, and sand characteristics may influence irrigation success. Effects diminish with depth and embryonic responses vary with species and the timing of irrigation during embryos development (Gatto et al., 2023). Additionally, the duration and frequency of irrigation, together with the volume of water applied influence the cooling achieved and potentially embryonic survival. Effective irrigation is crucial to maximize cooling and minimize risks of nest inundation or fungal growth and the aim of the irrigation must be clearly set, either targeting biased sex ratios or inadequate moisture.

Integrated approaches combining multiple strategies provide the most robust protection for turtle nests (Fuentes et al., 2012; Jourdan & Fuentes, 2015). All strategies listed above have been assessed feasible and cost effective (Clarke et al., 2021) but their success depends on the fact that they need to be tailored to each nesting ground, considering a variety of factors and environmental conditions.

3.3 Local climate variations effects on sea turtles reproductive outputs

Because the effectiveness of conservation strategies is highly dependent on prior environmental conditions, it is essential to guide tailored management and understand the future impacts of climate change at nesting grounds. Numerous studies have examined the effects of temperature variations on sex ratios, embryos lethal threshold, or hatchling quality within nests (Matsuzawa et al., 2002; Howard et al., 2014; Hays et al., 2017; Booth, 2017; Santidrián Tomillo & Spotila, 2020), but only a few studies to date have looked at the effects of local climate on the reproductive outputs of in situ sea turtles nests (n=5, listed in Table 3.1). Yet is it likely that the effects of climate change on hatchling production may be of great impact on population stability (Santidrián Tomillo et al., 2015; Laloë et al., 2017; Montero et al., 2018).

Studies have primarily looked at the effects of air temperature and precipitation, with variability observed at each study site. Reproductive outputs are usually measured in hatching success, or the number of eggs that have hatched within one nest versus those that did not hatch, and emergence rates, or the number of hatchlings that have made it out of the nest versus those who died. In the eastern Pacific, ENSO (El Niño Southern Oscillation) cycles are significantly correlated with hatching success and emergence rates of leatherback nests, where warmer and drier conditions associated with El Niño events negatively impact egg and hatchling survival (Santidrián Tomillo et al., 2012). Long-term precipitation increases leatherback hatchling outputs at regions with dry climatic conditions, but the effects of precipitation vary in areas with high precipitation and are unclear in temperate climate (Santidrian Tomillo et al., 2015). The development stage of embryos also plays a role, with increased mortality associated with decreased precipitation and higher temperatures at late stage of development, whereas precipitation prior to, and during stage zero (upon laying the eggs) have the greatest influence on early mortality (Rafferty et al., 2017). Additionally, leatherback deeper nests suffer higher mortality following prolonged rainfall events that significantly increase the water table and sand moisture levels at Pacuare reserve, Costa Rica (Rivas et al., 2018).

Across Brazil, warmer temperatures negatively affect hawksbill turtles nests while precipitation generally have a positive impact on hatchling production. This suggests that moisture can mitigate some of the negative effects of higher temperatures by cooling the sand, benefiting areas with inadequate moisture levels (Montero et al., 2018b). Similar studies showed variable effects of climatic factors on loggerhead nests, depending on the nesting beach and region (Montero et al., 2019). While air temperature effects were unclear, precipitation had negative effects on hatching success, but positive effects on emergence rates. This could mean that overly moist sand is detrimental for the development of embryos, while excessively dry sand create challenging conditions for hatchlings to emerge from the nests. Effects of higher temperatures were generally negative at tropical grounds but rather positive at more temperate Brazilian grounds. At other temperate grounds in Florida, humidity had negative influence of the development of loggerhead eggs, probably due to the already high humidity levels during nesting season. Precipitation and air temperature had a negative effect at the warmer and wetter site, but a positive effect at the other cooler and dryer site (Montero et al., 2018a). In a study carried out at grounds where both hawksbill and olive ridleys lay their eggs, the two species required a different amount of precipitation and humidity levels to notice positive effects on hatching success (Bomfim et al., 2021).

Study	Species (RMU)	Local climate factors	Reproductive outputs	Methods	Key results
Santidrian Tomillo et al. (2012)	Leatherback (East Pacific)	Air temperature and monthly precipitation	Hatching success and emergence rates	Used Generalized Linear Models (GLMs) to analyze effects of air temperature and rainfall on leatherbacks reproductive outputs.	Found drier and warmer conditions associated with ENSO cycles to negatively affect reproductive outputs. Used global climate model projections and predicted significant declines in reproductive output throughout the 21st century (Costa Rica).
Santidrian Tomillo et al. (2015)	Leatherback (Northwest Atlantic; East Pacific; Southwest Indian)	Air temperature and monthly precipitation	Hatching success and emergence rates	Used Generalized Additive Models (GAMs) to analyze effects of air temperature and rainfall on leatherbacks reproductive outputs.	Found variable effects across sites. High air temperatures reduced reproductive output at dry sites, while increased precipitation was beneficial. Decreases in reproductive outputs predicted at the tropical study sites (Central America) and increases at the temperate study site (South Africa).
Montero et al. (2018a)	Loggerhead (Northwest Atlantic)	Air temperature, rainfall, SST, wind speed and air moisture	Hatching success and emergence rates	Used Generalized Linear Mixed-Effects Models (GLMERs) to analyze the effects of five local climate variables on loggerheads reproductive outputs.	Moisture, precipitation and temperature had negative effects at the warmer and wetter site, and positive effects at the cooler and dryer site. Did not find influence of SST and wind speed. Predicted increases in hatching success until 2100 (Florida).

Montero et al. (2018b)	Hawksbill (Southwest Atlantic)	Air temperature, accumulated rainfall, average rainfall, air moisture, solar radiation and wind speed	Hatching success and emergence rates	Used Generalized Linear Mixed-Effects Models (GLMERs) to analyze the effects of five local climate variables on hawksbills reproductive outputs.	Identified air temperature and precipitation as main drivers of HS and solar radiation as main driver of ER. Warmer conditions and higher solar radiation had negative effects on nests, while wetter conditions had a positive effect Predicted decreases in hatching success until 2100 (Northern Brazil).
Montero et al. (2019)	Loggerhead (Southwest Atlantic)	Air temperature, rainfall, air moisture, wind speed and solar radiation	Hatching success and emergence rates	Used Generalized Additive Models to analyze the effects of six local climate variable on loggerheads reproductive outputs.	Identified air temperature and rainfall as main drivers, wih variability of effects across sites. No strong effect of SST and wind speed. Predicted decreases in hatchling production at tropical sites (North Brazil) and increases at more temperate sites (Rio de Janeiro).

Table 3.1 : Studies that modelled the effects of local climate variable on reproductive outputs of sea turtles (*in situ* nests) and their main findings.

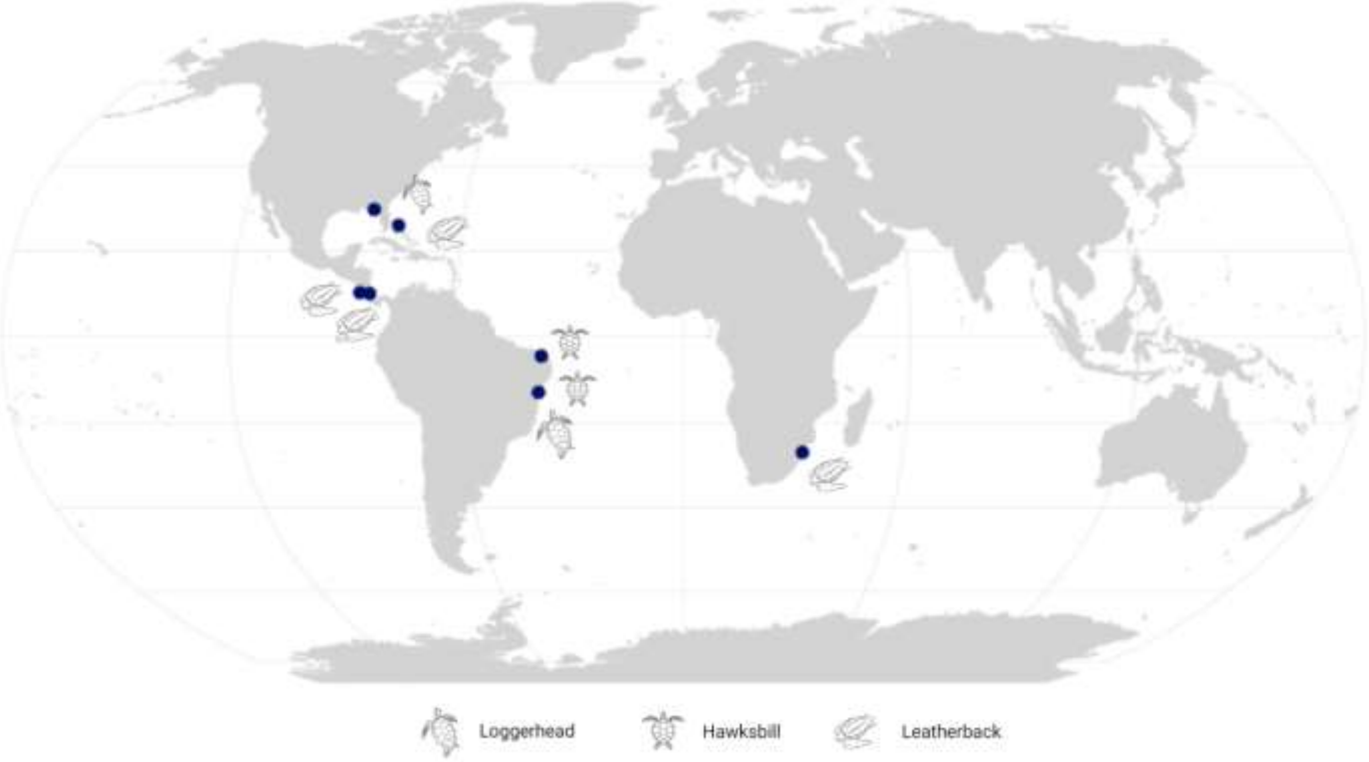


Figure 3.1 : Study sites (Playa Grande, Costa Rica; Pacuare, Costa Rica; Sandy Point, Bahamas; St George Island, Florida; Rio de Janeiro, Bahia, Espirito Santo and Rio Grande do Norte, Brazil; Maputaland, South Africa) included in previous studies that modelled the effects of local climate on sea turtles reproductive outputs from in situ nests (listed in **Table 3.1**).

In all studies, humidity, precipitation and/or air temperature are the main drivers of reproductive outputs, excepted in Montero et al. (2018b) who identified solar radiation as the main driver of hawksbill’s emergence rates in northern Brazil, with a negative effect on hatchling production. This is likely due to the proximity with the equator that results in high solar radiation significantly increasing sand temperature and drying out the sand: an excessively dry sand may cause cave-ins during hatchlings’ ascent out of the nest. Solar radiation also has negative effect on loggerhead emergence rates in Brazil, although it was not the primary driver (Montero et al., 2019). Less studied factors such as wind speed and sea surface temperatures, showed minimal effects on nests (Montero et al., 2018b, 2019).

To predict how sea turtle embryos will respond under various climate change scenarios, studies have used linear and additive models to analyze the effects of local climate variations on reproductive outputs and applied their results to global IPCC projections. This allows to anticipate how specific populations might respond in the future at specific nesting grounds. The results varied by location, with temperate grounds predicted to fare differently and potentially more positively than tropical regions, whose temperatures are already close to thermal limits of sea turtles embryos. Significant decreases in reproductive outputs are expected throughout the century in Central America and the Caribbean, areas that already present challenging conditions for egg development, and experience "boom and bust" recruitment cycles due to ENSO variations (Santidrian Tomillo et al., 2012, 2015). For both loggerhead and hawksbill nesting beaches in northern Brazil, decreases in reproductive success are expected, whereas southern, more temperate, Brazilian grounds may benefit from increases in temperatures (Montero et al., 2018a, 2019). Similar positive projections were found at temperature grounds in Florida and South Africa, where increase in hatchling production is expected before 2100, provided that contingent factors such as humidity and precipitation do not reach harmful levels (Santidrian Tomillo et al., 2015; Montero et al., 2018b & 2019).

3.4 : Implications and knowledge gaps

Is it clear that the effects of climate change on sea turtles nests will be site-specific. To inform management and implement effective conservation, it is crucial to understand the potential impacts for each population. It is still unclear whether all different sea turtles species have similar responses to changes in their environment; thermal thresholds may vary between species (Howard et al., 2014) and differences were found in how precipitation affects hawksbill and loggerhead nests at grounds were both species nest, although this may be attributed to differences in nesting seasonality (Montero et al., 2018b). All studies to date that have explored the effects of local climate on nests have focused on single species, with no research comparing effects of across different species sharing a nesting ground. This thesis proposes to build from previous work and explore how variations in local climate affect nests at shared nesting beaches. One hypothesis is that species responses are similar, and the effects of local climate are mainly dependent on the characteristics of the site where eggs are laid. The second hypothesis is that responses are also species-specific and that this needs to be considered when implementing management at nesting grounds.

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MANUSCRIPT

Variability in the effect of climate parameters on the reproductive outputs of sea turtles that share nesting grounds

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Key words: sea turtles, climate change, hatching success, emergence rate, reproductive outputs, scientific modeling

ABSTRACT

Climate change is expected to impact animals whose life history traits are reliant on environmental parameters. This is the case for sea turtles, who lay their eggs at temperate and tropical beaches and have the development of their embryos dependent on environmental conditions at their nesting grounds. Understanding how sea turtles reproduction will be impacted by climate change is crucial to guide effective management and help maintaining sea turtle populations. Studies that have explored the effects of local climate variables on sea turtles reproductive outputs have focused on individual species, with no research to date comparing effects across species that nest at the same location and under similar conditions. We address this knowledge gap by comparing the effects of climate variables on nests from different species at shared nesting grounds. We used Generalized Additive Models (GAMs) to explore how air temperature, sand temperature, precipitation and humidity affect reproductive outputs of *in situ* nests of loggerhead (*Caretta caretta*), leatherback (*Dermochelys coriacea),* hawksbill (*Eretmochelys imbricata*) and olive ridley (*Lepidochelys olivacea*) sea turtles. Our results show variability in the response of species that nest at the same location with the same seasonality. We conclude that embryos response to local climate is also species specific and therefore, conservation efforts at nesting grounds should take into consideration not only the conditions at each site but also the requirements of each species.

I. INTRODUCTION

Changes in the world’s climate are occurring at an unprecedented rate and will impact species that are heavily reliant on environmental parameters (Foden et al., 2013; Intergovernmental Panel on Climate Change, 2021). This is the case for sea turtles, since their life-history, behavior, and physiological traits are strongly influenced by environmental factors (Standora & Spotila, 1985). Their reproductive output is driven by local environmental conditions at their nesting grounds, as incubation temperature, sand moisture levels and rainfall events significantly impact incubation length, hatchling development and hatching success (Matsuzawa et al., 2002; Howard et al., 2015; Booth, 2017; Rivas et al., 2018; Matthews et al., 2021;Fuentes et al., 2024). Sea turtle eggs must incubate within a narrow temperature range (~25°C to 35°C; Standora & Spotila, 1985; Howard et al., 2014) outside of which embryos do not develop and hatching success significantly decreases (Matsuzawa et al., 2002, Turkozan et al., 2021). Prolonged rainfall events and excessive moisture can lead to hatchling mortality (Rivas et al., 2018) and unusually high or low incubation temperatures tend to produce higher proportions of unfit hatchlings with impaired chances to reach the open sea and ultimately, adulthood (Burgess et al., 2006; Kobayashi et al., 2018). Sea turtles also have temperature-dependent sex determination (TSD) where incubation above a specific pivotal temperature (usually found between 29°C and 30°C; Hawkes et al., 2009) produces more females and below more males in the nest (Bull & Vogt, 1979).

Given their reliance on environmental parameters, all sea turtle species will be directly and indirectly affected by climatic changes, with impacts varying geographically, temporally, and between species and populations (Patrício et al., 2021; Fuentes et al., 2024). The important ecological roles they serve at both their nesting and foraging habitats (Bjorndal & Jackson, 2002) and their endangered status (IUCN Red List of Endangered Species) make them species of important conservation concern. Thus, there is a clear need to understand how climate change will impact sea turtles, specifically, an understanding of how changes in our climate will impact their reproductive output is needed to determine long-term population stability and guide appropriate conservation efforts.

As a result of this, several studies have explored how different climate variables affect hatching success and emergence rates of sea turtle eggs, with variability in the effects around the world and across species and populations (Santidrián Tomillo et al., 2015; Rivas et al., 2018; Montero et al., 2018a,b, 2019; Bomfim et al., 2021). Research to date have mainly focused on how air temperature and rainfall affect reproductive outputs and found warmer conditions at temperate nesting grounds to have positive effects on hatching success, while increases in temperature in warmer or tropical areas tend to have negative effects due to the eggs already incubating near their upper thermal threshold (Santidrián Tomillo et al., 2015; Montero et al., 2018a). Similarly, variability exists on the effects of precipitation on the hatching success of sea turtle species with mild rain having a positive effect on hawksbill (*Eretmochelys imbricata*) in northern Brazil when olive ridley (*Lepidochelys olivacea*) required prolonged rainfall to have a positive effect on hatching success (Bomfim et al., 2021). In Costa Rica and Florida, rainfall was associated with negative effects on leatherback (*Dermochelys coriacea*) and loggerhead (*Caretta caretta*) nests respectively (Lolavar & Wyneken, 2015; Rivas et al., 2018). It is thought that increases in moisture can have beneficial effects in dry areas and increase emergence rates where the grounds natural moisture levels are not adequate (Montero et al., 2018, Lolavar & Wyneken, 2021). However, they should not exceed a certain threshold since excessive moisture decreases emergence success and fitness of developing turtles, impacting their ability to swim and successfully disperse out of the nest (Matthews et al., 2021; Martins et al., 2022) and favors excessive microbial development within the nests (Bézy et al., 2015).

It is clear that variability exists on how climate variables affect hatching success and emergence rate of different species and populations of sea turtles globally. However, these differences may be attributed to studies being conducted at different nesting grounds, which experience different environmental conditions. All previous studies that have explored the effects of climate variations on nest productivity have focused on a single species, with no research to date comparing effects across species sharing a nesting ground. To address this knowledge gap, we expand from previous work and compare these effects on several species at shared rookeries. This will provide further insights on species specific responses from different climate parameters. This knowledge is essential to predict future impacts of climate change on sea turtle populations and guide effective management at nesting grounds.

II. METHODS

Study sites and species

Our study was conducted in coastal areas in Brazil, which are largely used as nesting ground by five out of the seven existing species of sea turtles: the loggerhead sea turtle (*Caretta caretta*), the green sea turtle (*Chelonia mydas), the* olive ridley sea turtle (*Lepidochelys olivacea*), the hawksbill sea turtle (*Eretmochelys imbricata*) and the leatherback sea turtles (*Dermochelys coriacea)* (Marcovaldi & Dei Marcovaldi, 1999). Once largely exploited, Brazilian sea turtles stocks displayed a fast recovery following the implementations of conservation legislations in the 1980s and the creation of Projeto Tamar (https://www.tamar.org.br/), a public marine conservation institute monitoring turtle activity in nearly every coastal states in Brazil (Marcovaldi & dei Marcovaldi, 1999; Marcovaldi & Chaloupka, 2007. With climate projections for this area including rising temperatures and increases in the frequency and intensity of heavy rainfall events (Avila-Diaz et al., 2020) a decrease in sea turtles reproductive success is expected in most areas under climate change scenarios (Montero et al., 2018, 2019; Fuentes et al., 2024).

Data for this study was obtained through daily beach patrols conducted by Projeto Tamar between September 2013 and December 2020 across 3 important nesting beaches in Brazil from 3 states (Figure II.1). The data included information on nests laid by four different sea turtle species: loggerhead sea turtles, olive ridley sea turtles, hawksbill sea turtles and leatherback sea turtles (Table II.1, Figure II.1). Collected data included nest location (latitude and longitude), lay date, hatch date and hatchling production (number of hatched and unhatched eggs + number of live and dead hatchlings within the nest).

Reproductive output was assessed by determining hatching success (HS) and emergence rate (ER) values. HS and ER were calculated with the following:

$$HS = (\text{Total number of eggs} - \text{Unhatched eggs}) / \text{Total number of eggs}$$

$$ER = (\text{Hatched eggs} - \text{Dead hatchlings}) / \text{Hatched eggs}$$

as per Montero et al., 2018. Only nests with complete climate data available throughout the whole incubation time were included in the study and nests with missing climate data during incubation time were not included in the modeling analysis. We also did not consider nests that experienced disturbances (e.g., depredation and storm-related impacts).

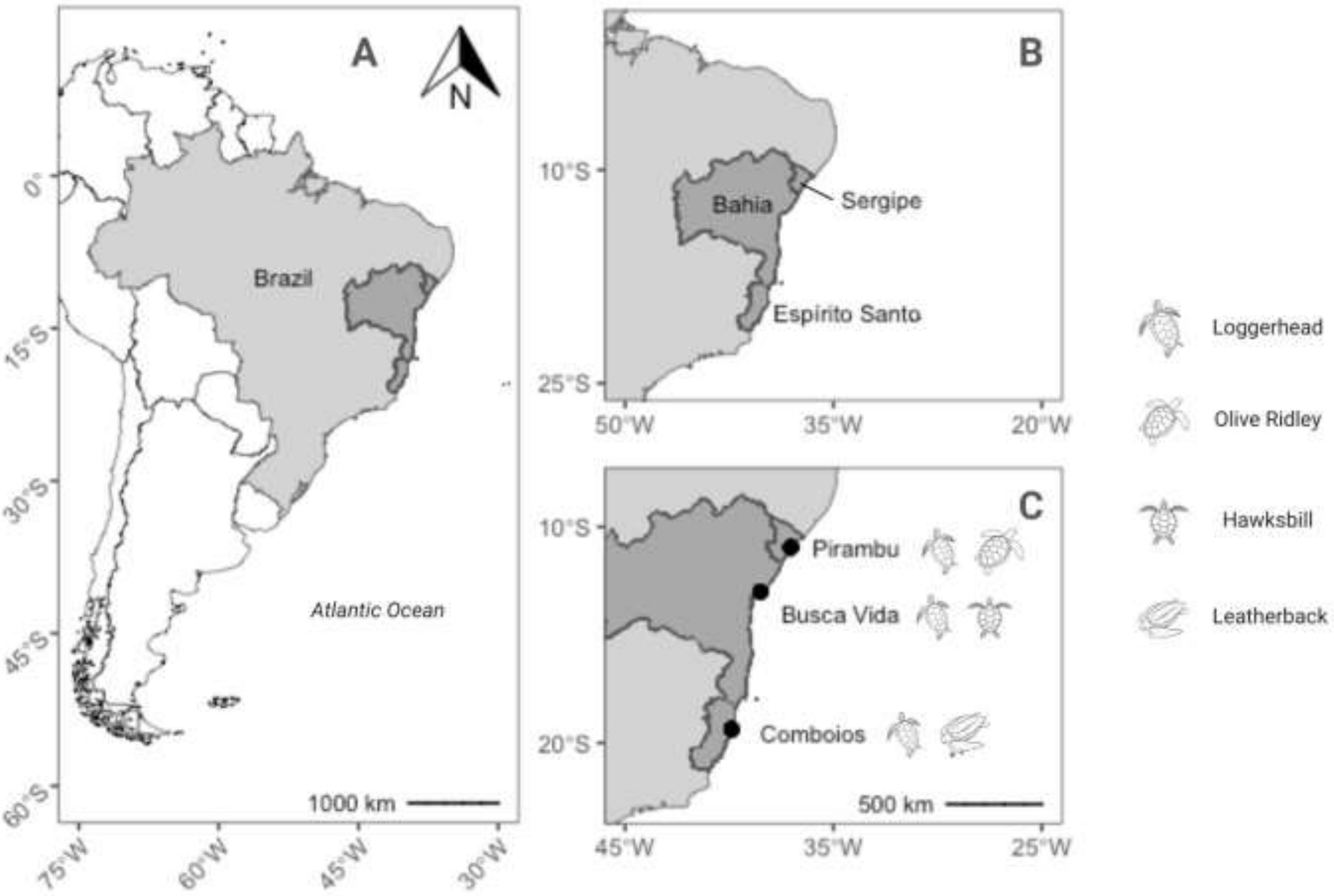

Figure II. 1 : Map showcasing our three study sites in A) Brazil, B) in relation to each state (Sergipe, Bahia and Espirito Santo), and C) their location within the coast and the sea turtle species nesting at each site.

Table II. 1 : Undisturbed nests (N total = 4739) considered for each species in the 3 study sites and the associated weather station used to retrieve the climate data, with their respective distances from the study sites. Nests were selected based on having complete nest information and climate data available for the whole incubation time and up to two months prior to the nest being laid.

Beach (n months)	**Pirambu (n =24)**		**Busca Vida (n = 30)**		**Comboios (n = 55)**	
Weather station	Aracaju (33km)		Salvador (31km)		Linhares (49km)	
Species	Loggerhead	Olive ridley	Loggerhead	Hawksbill	Loggerhead	Leatherback
2013	3	50	22	1	57	38
2014	43	404	49	30	290	13
2015	65	451	134	22	507	21
2016	9	376	130	23	251	19
2017	20	249	97	14	119	10
2018	37	336	-	13	60	31
2019	45	498	-	40	-	9
2020	13	71	-	7	-	41
Total	**235**	**2435**	**432**	**150**	**1284**	**182**

Climate variables

Four climate variables were considered in the study: sand temperature (C°), air temperature (C°), accumulated rain (mm) and humidity (%). Sea surface temperature (°C) and wind speed (m/2) were previously found not to significantly affect the reproductive output of sea turtles in Brazil (Montero et al. 2019) and thus those variables where not considered here. Sand temperature was obtained by Projeto Tamar who deployed temperature data loggers (Vemco Logger VUE minilogger II; accuracy ± 0.5°C, and resolution: 0.0625 °C) across each nesting beach at depths equivalent to sea turtle nest. Air temperature, accumulated rain and humidity values were retrieved directly from the Brazilian National Institute of Meteorology (INMET; http://www.inmet.gov.br/portal/). INMET provides weather data collected from stations positioned all over the country. Weather stations were selected based on their proximity to our study sites, with only coastal weather stations being considered (Table II.1). For all climate variables, hourly data was converted into daily and monthly values for further analysis.

Analysis

Hatching success and emergence rates were arcsine transformed to reduce skewness and approach normality, as per Montero et al. (2019). Since normality was not reached in the distributions, non-parametric tests were used to perform comparisons across locations and species. Levene's test with center mean was used to test homogeneity of variances; Kruskal-Wallis test was used to test differences between the groups and a post-hoc pairwise Wilcoxon test using a Bonferroni correction allowed us to compare each pair of species within each nesting beach and differences in local climate between locations. We used RStudio version 4.2.2 for all statistical analyses.

Generalized Additive Models (GAMs) were used to explore the relationship between the hatching success, emergence rate and the considered climate variables. GAMs work as an extension of generalized mixed linear models (GLMERs) that offer the flexibility to capture potential non-linear and interactive effects of predictors. The model predictors (climate variables) were explored at six different temporal scales: 1) the last month of incubation (hatch_variable); 2) the whole period of incubation (inc_variable); 3) the month nests were laid (0_variable); 4) the month nests were laid plus the month before laying (0.1_variable); 5) the month nests were laid plus two months prior to laying (0.2_variable) and 6) only the two months before nests were laid (1.2_variable). The rationale behind investigating climatic conditions before the incubation started is based on the hypothesis that the state and characteristics of the sand at the time of nest deposition may have been shaped by earlier local climatic conditions and may influence incubation conditions. The models were fitted using a binomial distribution (number of hatched eggs versus not hatched for hatching success; alive versus dead hatchlings for emergence rate), as per Montero et al., 2019. The smoothness parameter was set using the REML method (Wood, 2006) with the significance level set at $\alpha = 0.05$. To select models with the best goodness of fit and predictive accuracy, we looked at AIC (Akaike Information Criterion) and deviance values (Tomillo et al., 2015; Montero et al., 2019). The AIC is an estimator that measures goodness of fit relative to the complexity of the model, while deviance is a percentage indicating what proportion of variation in the data is captured by the model (Akaike, 1974). All statistical analyses were conducted in RStudio version 4.2.2. and the 'mgcv' package was used for our models (Wood, 2006).

III. RESULTS

Reproductive outputs

A significant difference was found in hatching success (HS) and emergence rate (ER) between each species at each of our study sites (Wilcoxon Mann-Whitney test, p < 2.2e-16 at Pirambu and Busca Vida for both HS and ER; in Comboios p_value = 2.657e-06 for HS and p_value = 0.01237 for ER). Overall, olive ridley was the species with the best nest performance and the most nests laid, and hawksbill was the species that has the lowest nest performance and the one with the least nests analyzed (Figure III.1). When comparing species nesting within the same beach, olive ridleys had higher reproductive output (HS = 86.9%, ER = 97.9%) compared to loggerheads (HS = 74.1%, ER = 93.8%) in Pirambu. Loggerheads had higher reproductive output (HS = 88.32% and ER = 86.15%) than hawksbills (HS = 78.7%, ER = 77.46%) in Busca Vida. In Comboios beach, loggerheads had higher HS (80.59%) than leatherbacks (75.2%), but leatherbacks had a slightly better ER (94.62%) than loggerheads (93.2%). At Pirambu beach and Comboios beach, ER for both species were higher than HS, which was not the case at Busca Vida beach, where ER values of both species were slightly lower than HS (Figure III.1).

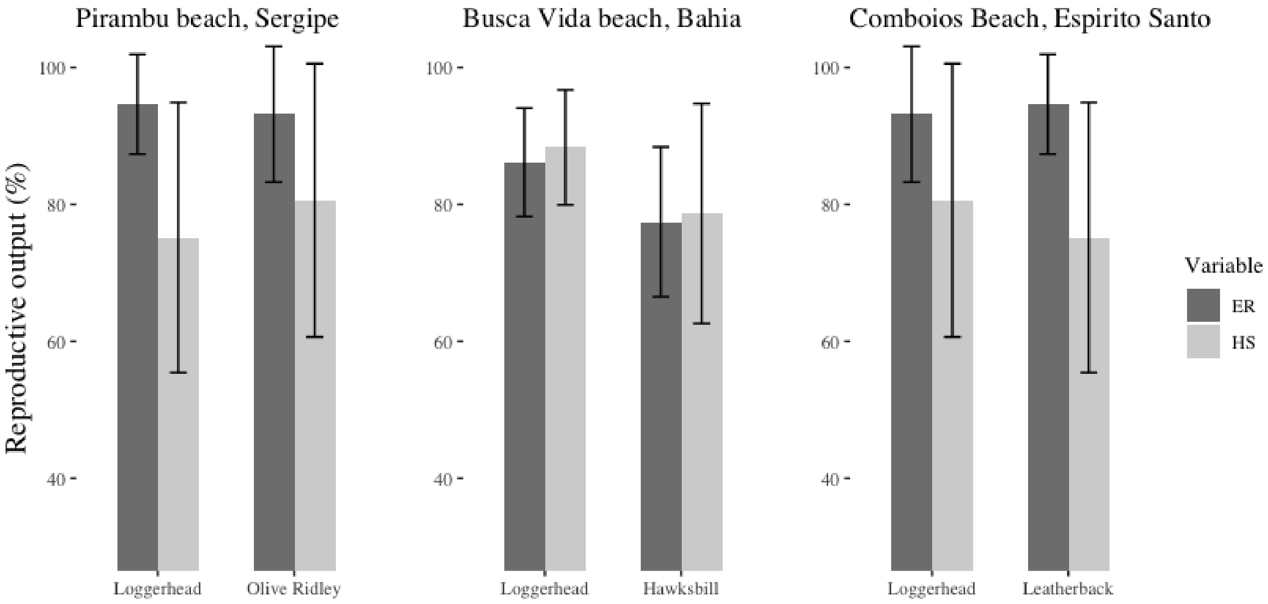

Figure III.1: Reproductive output of each sea turtle species at our study sites. Hatching success (light gray) and emergence rate (dark gray). Error bars show standard deviation values.

Nesting seasons and local climate

In Pirambu beach, the northernmost and closest nesting site to the equator, loggerhead and olive ridley turtles had similar nesting seasons with the peak of their nesting season (December-January) aligning with the warmest and driest time of the year (Figure III.2). The peak of the incubating season occurred from February-March, which aligned with the start of the wet season (Figure III.2, a,b,c). Olive ridley nests were recorded during every month of the year, whereas the loggerhead nesting season occurred from September to April with a peak during the onset of summer and most eggs incubating during the warmest time of the year. The wettest months of the year coincided with the least nests laid for both species (Figure III.2).

In Busca Vida beach, loggerhead turtles nested evenly (no peak) during the whole dry season (September to March) with some nests incubating during the beginning of wet season. Hawksbill turtles nests were laid from November to May, with the peak of their nesting season (January-March) coinciding with the warmest months of the year and the peak of their incubation season aligning with the wet season (Figure III.2 d,e,f). The wettest months (April and May) coincided with an abrupt decrease in hawksbill nesting, and no nests laid for loggerhead.

In Comboios beach, the southernmost nesting beach, loggerhead and leatherback turtles had shorter nesting seasons with the peak of nesting (October-December) for both species aligning with the wettest months of the year, and the peak of the incubation season (December-January) aligning with a decrease in rainfall and increasing temperatures (Figure III.2 g,h,i). For both species, most nesting happened during the coolest and wettest months (between October and December).

There were significant differences in overall climate between all study sites. Not all climate variables were significantly different between sites. Post-hoc pairwise comparisons found significant differences between Pirambu and Busca Vida in air temperature values (p_value = 9.1e-05) and humidity levels (p_value = 6.2e-15) but not in sand temperatures (p_value = 1) and rainfall (p_value = 0.21997). Busca Vida and Comboios had significant differences in sand temperatures (p_value = 0.00051), air temperatures (p_value = 9.1e-05) and rainfall (p_value

= 0.00021) but not in humidity levels (p_value = 0.079). Pirambu and Comboios had significant differences in sand temperatures (p_value = 1.5e-06), air temperatures (p_value = 2.9e-11) and humidity levels (p_value = 1.3e-11) but not in rainfall (p_value = 0.14697).

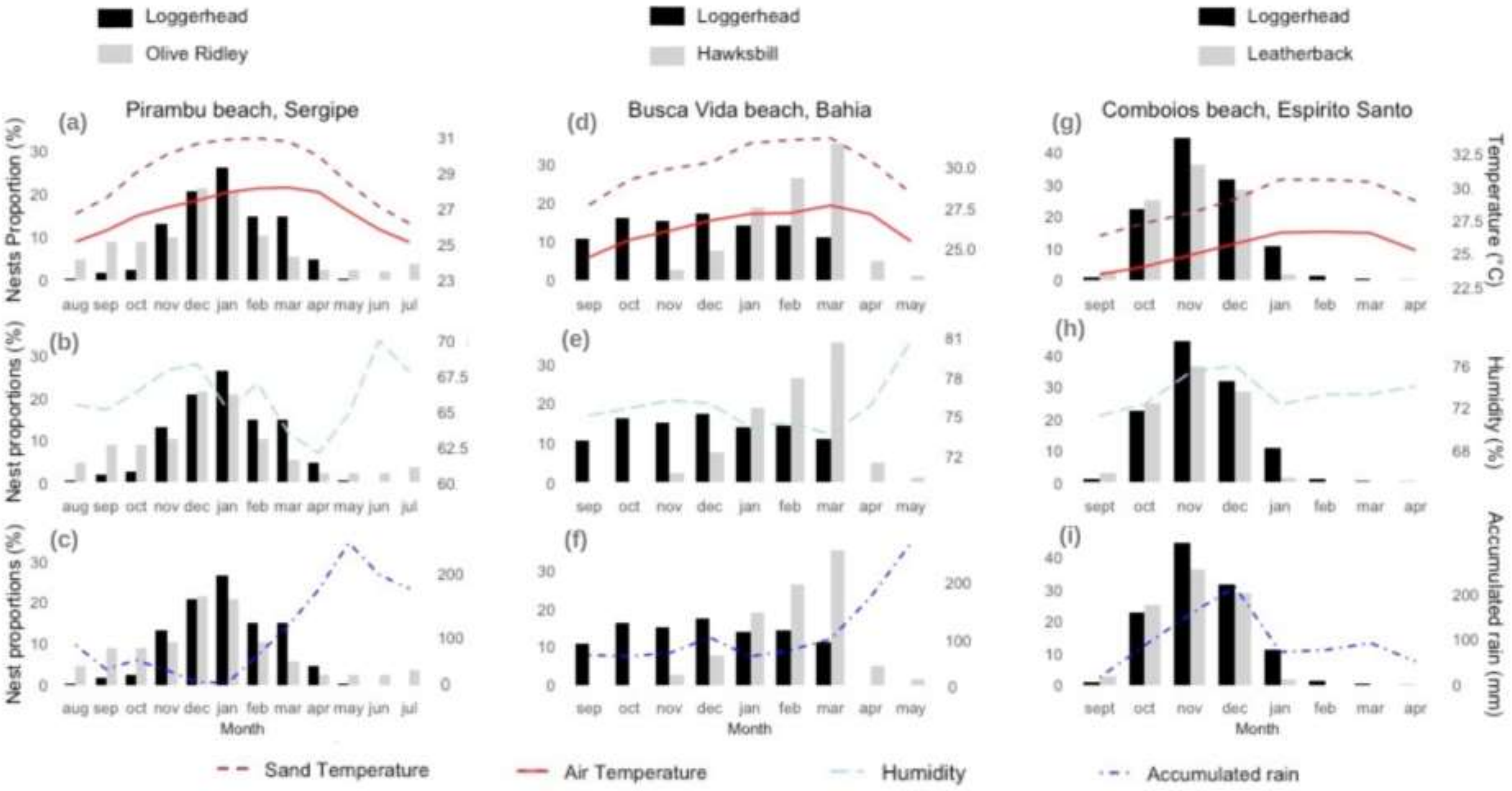

Figure III.2: Nests proportion versus climatic conditions in Pirambu beach - (a), (b) and (c) - Busca Vida beach - (d), (e) and (f) – and Comboios beach - (g), (h) and (i). Bars show monthly proportions of nests laid for both species at every location and lines represent climate variables recorded at the weather stations. Panels (a), (d) and (g) show mean monthly values of sand and air temperature, panels (b), (e) and (h) display humidity values and panels (c), (f) and (i) show mean monthly accumulated rain values (mm).

Hatching seasons

In Pirambu beach, olive ridley eggs hatch throughout the year whereas loggerhead nests hatch from November to June (Figure III.3 a,b). Olive ridleys present relatively high hatching success (> 80%) with a slight decline for nests that hatch in July and August (Figure III.3 a), whereas hatching success for loggerheads nesting in the same beach is lower across all months, especially in March and April (Figure III.3 a). Similarly, emergence rate for olive ridleys was higher than for loggerheads nesting at the same beach (Figure III.3 b).

In Busca Vida beach, loggerhead nests hatch from November to May whereas hawksbill nests hatch from December to May (Figure III.3 c,d). Loggerhead turtles displayed higher reproductive output than hawksbill nests in the same beach throughout the whole season.

In Comboios beach, leatherback turtles have the shortest nesting season with eggs hatching between December and February, whereas loggerhead nests hatch from November to April (Figure III.3 e,f). Loggerheads had higher hatching success values than leatherbacks throughout the whole season, but slightly lowest emergence values when compared across the same beach (Figure III.3 e,f).

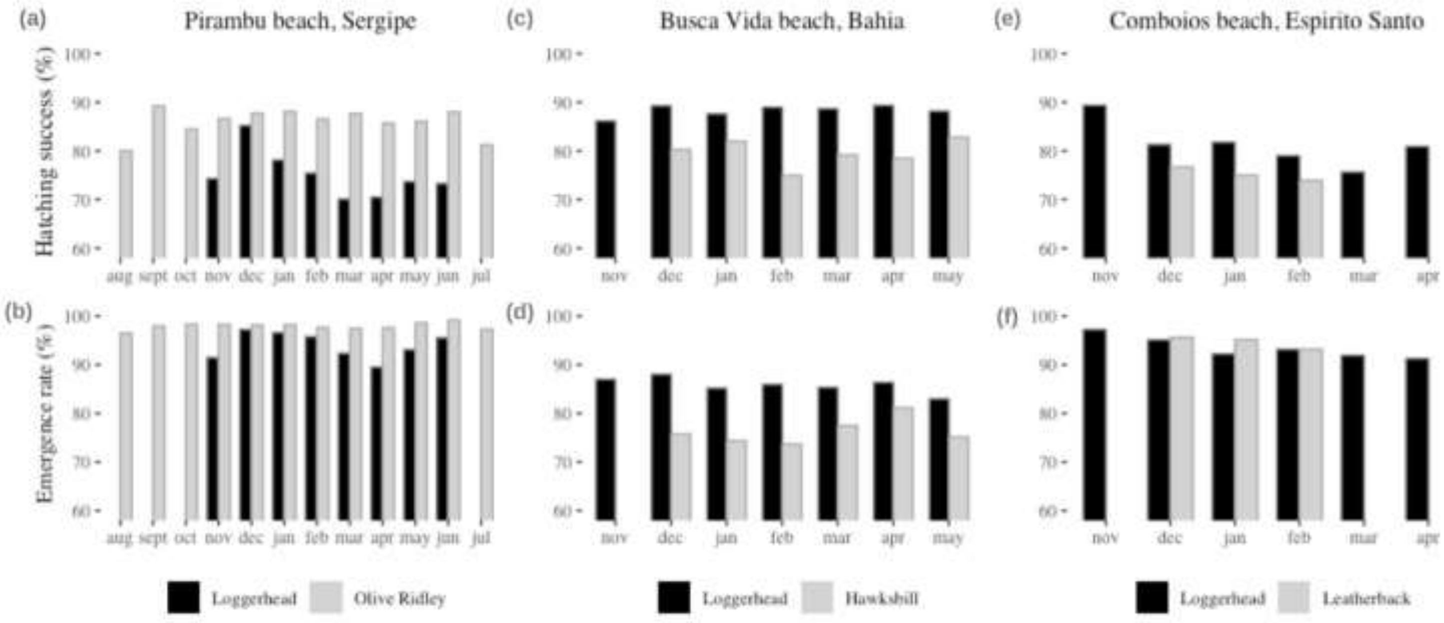

Figure III.3: Monthly mean hatching success and emergence rate during the hatching season at our study sites: (a, b) Pirambu beach, (c,d) Busca Vida beach and (e,f)), Comboios beach. *Note*. Only months with at least 3 hatched nests recorded appear in the graphs.

Effect of local climate – Results of the GAM analysis

The best predictors describing HS and ER varied by species and location (Table III.1, Figure III.4). The highest deviances explained were always reached with a combination of the four climate predictors (air temperature, sand temperature, rainfall and humidity) at different time scales throughout the nesting events. Higher sample sizes (species with more nests) decreased models fit (higher AIC and lower deviances explained). The time scales explored ranged from up to two months before the start of the nesting event, until nest emergence. Most GAMs showed an influence of one or several predictors up to one month prior to the eggs being laid (Table III.1, Figure III.4).

Table III.1 : Results (p_values, r-squared and deviance values) for each of the best fit GAMs for each species within their study site. Note. 0 = laying month. R. output = reproductive output.

Species (location)	R. output	Variable	AIC	R-squared	p_value	Deviance
Loggerhead (Pirambu)	HS	rain_0	5516	0.0374	<2e-16	18.9%
		sand_inc			<2e-16	
		airtemp_0			<2e-16	
		humid_hatch			<2e-16	
	ER	airtemp_0-1	2058	0.143	<2e-16	28%
		sand_0			<2e-16	
		humid_hatch			<2e-16	
		rain_0			<2e-16	
Olive Ridley (Pirambu)	HS	sand_inc	49284	0.0093	<2e-16	3.08%
		airtemp_0-1			<2e-16	
		humid_hatch			<2e-16	
		rain_hatch			<2e-16	
	ER	sand_inc	11797	0.0171	<2e-16	4.65%
		humid_hatch			<2e-16	
		rain_inc			<2e-16	
		airtemp_0-1			<2e-16	
Loggerhead (Busca Vida)	HS	humid_hatch	3907	0.139	<2e-16	21.5%
		sand_0			<2e-16	
		rain_0-1			<2e-16	
		airtemp_inc			<2e-16	
	ER	humid_inc	3641	0.143	<2e-16	19.2%
		sand_0-1			<2e-16	
		airtemp_0			0.000298	
		rain_0-1			<2e-16	

Species (location)	**R. output**	**Variable**	**AIC**	**R-squared**	**p_value**	**Deviance**
Hawksbill (Busca Vida)	HS	sand_inc	1159	0.261	< 2e-16	55.5%
		rain_inc			< 2e-16	
		airtemp_inc			< 2e-16	
		humid_inc			< 2e-16	
	ER	rain_0-1	564	0.377	< 2e-16	57.5%
		humid_0-1			4.22e-06	
		sand_inc			7.25e-05	
		airtemp_inc			< 2e-16	
Loggerhead (Comboios)	HS	sand_inc	36513	0.0341	<2e-16	6.53%
		rain_inc			<2e-16	
		humid_hatch			<2e-16	
		airtemp_inc			<2e-16	
	ER	sand_inc	14002	0.0647	<2e-16	10.1%
		rain_inc			<2e-16	
		humid_hatch			<2e-16	
		airtemp_inc			<2e-16	
Leatherback (Comboios)	HS	airtemp_hatch	1050	0.248	<2e-16	52.9%
		humid_hatch			<2e-16	
		rain_hatch			<2e-16	
		sand_0-1			<2e-16	
	ER	sand_inc	451	0.287	5.35e-06	51.6%
		humid_inc			0.001469	
		rain_inc			0.000476	
		airtemp_inc			0.000147	

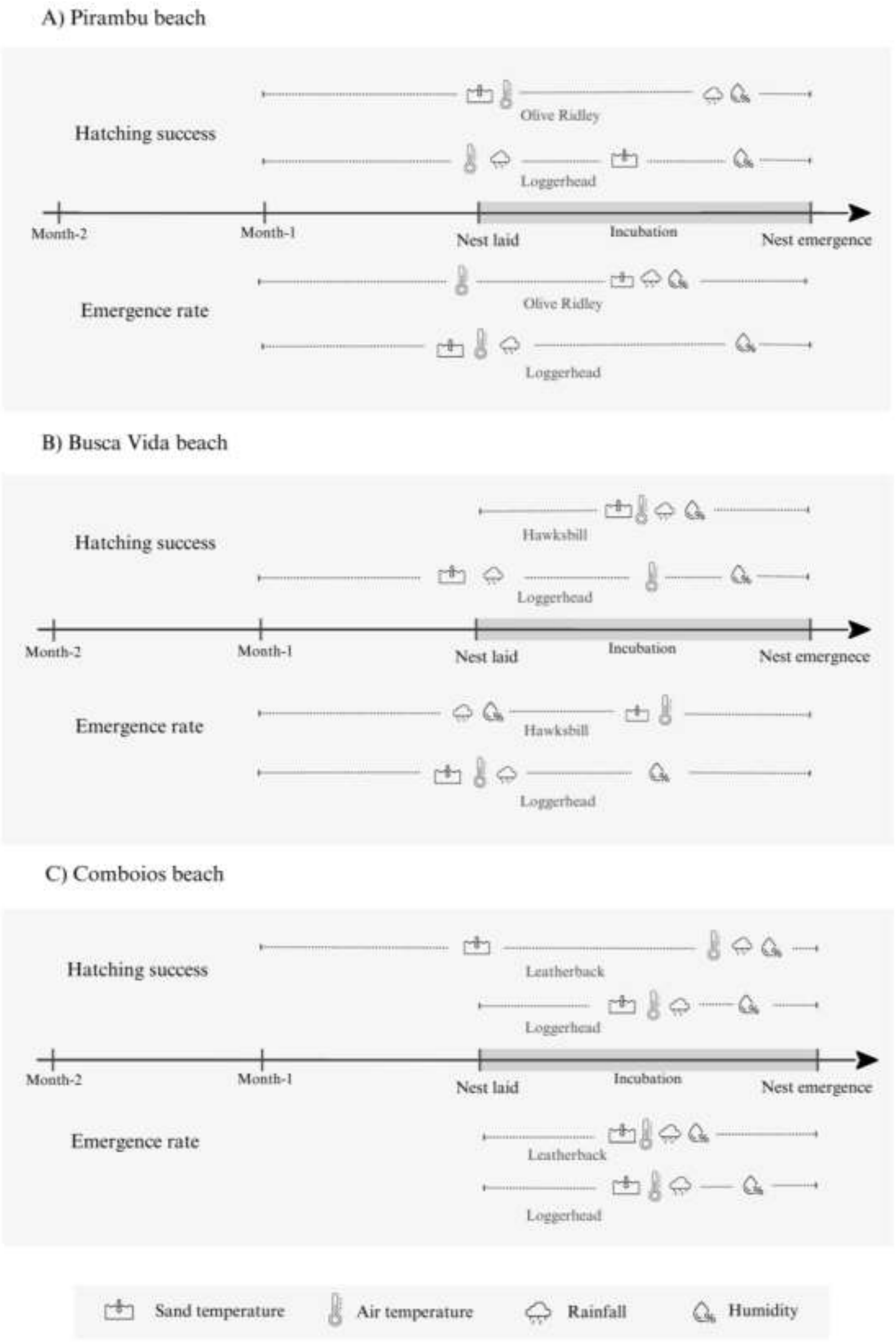

Figure III.4 : Timelines of the nesting event at each location, from two months before nests were laid up to emergence of nests. Symbols represent the time of the nesting event at which climate variables were found to have the most effect in our GAM analyses.

IV. DISCUSSION

The effects of climate variables on the reproductive output of sea turtles are species and site specific. They vary with species nesting at the same location and that have similar seasonality in their nesting season, with variability also found when the same species nests in different locations with the same seasonality. This highlights the importance of studies such as this one that are conducted at specific locations and for specific species without extrapolation of previous results to other species and locations. Such understanding of the complex relationships between climate variables and different species will be key to predict how species will be affected in the future.

Each of our study sites has a tropical climate with a dryer, warmer season and a wetter, colder season, although each site did not experience the same season at the same time (Pirambu and Busca vida had their wet season in January-July whereas Comboios happened in September-January). There were statistical differences in local climate between all locations but not all parameters were significantly different across beaches. No significant difference was found in sand temperatures between Pirambu and Busca Vida, in humidity between Busca Vida and Comboios, and in rainfall between Pirambu and Busca Vida or Pirambu and Comboios, but all locations had statistically significant differences in air temperature (see Table VII.2 of the supplementary material).

The best fit models were always obtained with a combination of the four climate predictors, suggesting that each of them influences reproductive outputs, and that their influences may be cumulative or have a synergetic effect. However, GAMs fit diminished with larger nests samples, and our larger samples had much lower deviance values compared to other similar studies (Table III.1). This indicates that other parameters than those included in the study may have influenced turtles nests in a significant manner. A variety of factors like clutch size, sediment characteristics (Fadini et al., 2011), vegetation cover (Cabrera Guerra et al., 2021), solar radiation (Montero et al., 2018b, 2019), tidal patterns and proximity to the high-water mark (Veelenturf et al., 2021) have the potential to influence embryo development and reproductive outputs. We did not take species-specific habitat preferences into consideration (for example hawksbill's tendency to nest in vegetated areas), but literature suggests minimal direct impact on reproductive output (Serafini et al., 2009). Our nest data did not indicate whether nests were infected with bacteria and fungi (high microbial activity, favored by broken eggs decomposition and high moisture levels, may lower hatching rates; Sarmiento-Ramírez et al., 2010; Bezy et al., 2015). Eggs can also be contaminated with varying levels of persistent pollutants after direct transfer from the mother which could affect hatching rates (Alava et al., 2006; Garcia-Besné et al., 2015). All nests in this study being in situ, although not depredated or impacted by storm they could have been exposed to unreported threats, like the ones induced by human presence. A more controlled approach, with nests relocated in protected nurseries, may allow to better monitor isolate the effects of climate parameters. Accuracy may also vary with distance between the study site and its associated weather station. Our GAMs revealed complex relationships between the climate variables and reproductive outputs (see supplementary material for all GAM plots – Figures VII.1 to VII.6). They also provided insights on the timescale at which each variable most influenced the nests (e.g. around the time of laying, the whole incubation or rather the end of incubation).

Each nesting location was predominantly used by two species of sea turtles, with occasional nests from other species recorded but not included in the study. The loggerhead sea turtle was the only species studied at all three locations, and they presented varying responses to climatic factors depending on the location, highlighting that the effects of local climate variations on nests are significantly dependent on the sand characteristics at the time the eggs are laid. This may also be reflective of the genetic diversity found within the loggerhead southwestern Atlantic Regional Management Unit (Wallace et al. (2023) identified two different loggerhead genetic stocks within that same RMU) that could influence the adaptive response of developing embryos (Maurer et al., 2021).

For loggerhead nests at Pirambu beach, where incubation predominantly occurs during the warm, dry season, increases in monthly precipitation and moisture levels were associated with decreased hatching success and emergence rates. In contrary, at Comboios, most incubation occurred during the rainy season and wetter, cooler conditions are associated with increased nest success. Loggerhead's nests in Busca Vida did not show a notable variation of monthly nest success with the different seasons. In our GAM analysis, lower air temperatures had a positive influence on hatching success on loggerhead nests at every location. This suggest that conditions at tropical grounds are already slightly too warm for loggerhead nests, and that a decrease in hatching success would be expected at those locations with projected increases in temperatures and precipitations for Brazilian nesting grounds under climate change scenarios. Previous work indeed predicted a decrease in loggerhead reproductive outputs at tropical Brazilian grounds but increases in reproductive outputs at more temperate grounds (Montero et al., 2019). The effects of other variables were unclear, although all predictors were significant. However, the GAMs did highlight a pronounced impact of humidity levels towards the end of incubation for both HS and ER in loggerhead nests at every location, while temperatures rather influenced the beginning of the incubation. This makes sense since it had already been demonstrated in leatherbacks sea turtles that embryos mortality in response to variations in precipitations can be dependent on the development stage of the eggs (Rafferty et al., 2017). Our results suggest that loggerhead eggs are influenced in the same way.

Hawksbill nesting seasonality at Busca Vida differed from loggerheads at the same location. There was a peak in nesting frequency during the warmest months (January to March), and an abrupt decrease in nesting as rain and moisture levels rise. Monthly mean reproductive outputs do not increase or decrease during the dry or wet season, although we expected hawksbill reproductive output to be favored by high levels of moisture (Flores-Aguirre et al., 2023). Montero et al. (2018) had found precipitation to influence positively hawksbill nests throughout Brazil, while warmer temperatures had a negative effect and suggested inadequate moisture levels of the sand, since their eggs are laid during the dryer months. In our GAM analysis, rain and humidity levels did not have a visible effect on reproductive output, even though both factors were significant. Rain and humidity at the beginning of the nesting event had the stronger effect on emergence rates, but their effect in unclear. Hawksbills in our study had a relatively low reproductive success compared to other species (both mean monthly HS and ER values remain below 80%). This can be partly due to the presence of hybrids from loggerhead-hawksbill inbreeding, which constitute an estimated 40% of the Brazilian hawksbill population: these hybrids often show lower reproductive success than their parental species, despite having similar nesting frequency or clutch sizes (Soares et al., 2017).

Our study includes the first analysis of local climate effects on olive ridley nests. Pirambu beach is a primary nesting area for olive ridleys in Brazil and they were the species with the highest number of nests recorded in a single location. Nests had high reproductive success. HS remained high throughout the whole year (>80%) but sightly decreased in July and August, coinciding with the lowest temperatures, highest rainfall and fewest nests laid. Emergence rates remained exceptionally high throughout the whole year (>97%) with a minor decrease in August (96,5%). This may indicate that temperature influences positively reproductive output, but this effect was not clearly visible in our GAMs. The models had low AIC values and deviances explained, despite all factors being significant (see Table III.1) and in general, reproductive outputs showed very mild variations in response to local climate (see GAM plots in the supplementary). HS was more influenced by air and sand temperatures around the time of laying and up to one month before, while precipitation and humidity influenced the end of incubation, with prolonged rainfall and high humidity levels showing slight negative effects on HS. Low sand temperatures had a negative effect on ER. In general, olive ridleys eggs seem to develop well in warm and dry conditions. They may not react negatively to predicted increases in temperature under climate change scenarios, but rather be challenged by the associated shifts in precipitation.

Leatherback turtles at our study site had a four-month nesting season with most activity occurring during the wettest and coolest time of the year. This differs from most other studies, where they usually nest during the warmer and drier times of the year (Santidrián Tomillo et al., 2012;2015). This is not uncoherent since sea turtles nesting seasons are triggered by oceanic cues (like SST and currents) rather than climatic conditions on land. Although being leatherbacks preferred nesting site in the southwestern Atlantic, a relatively small sample of nest was recorded during the seven nesting seasons studied (n = 182 in the whole study, n = 88 in the GAM analyses). Both HS and ER presented a slight decrease as temperatures rose and precipitation decreased, suggesting a negative impact of rising temperatures on nests but such effect is not visible in our GAMs. Previous research exploring the effects of air temperature and rainfall on leatherback nests found a positive effects of rainfall on HS at all sites and especially at tropical locations (Santidrián Tomillo et al., 2015)**.** In our GAM analyses, moderate amounts of rain had no visible effect on nests, but prolonged precipitations had a negative effect on both HS and ER. This could be due to the area already receiving an adequate amount of rain throughout the season, with additional rain pushing the suitable threshold for nests. Excessive rain can be harmful, as excessively high levels of moisture within nests may result in egg suffocation and reduce hatching success (McGehee, 1990). Also, effects of rain on leatherback nests may be long lasting and accumulate over time (Tomillo et al, 2015). Under climate change scenarios, increased precipitations and frequency in extreme weather events may pose the greatest challenge for leatherback nests.

V. CONCLUSION

Our study found variability in sea turtle nests response to climate parameters across species that nest in the same location. We expect all four species to be impacted differently following global warming projections at Brazilian nesting grounds. In the context of climate change, building a robust understanding of such interactions is crucial to develop appropriate conservation interventions and mitigate the effects that shifting climatic patterns will have on species that are reliant on environmental parameters. We aim to contribute to a baseline of information that will help predict future impacts and guide management at important sea turtle nesting areas.

ACKNOWLEDGMENTS.

We would like to acknowledge Projeto TAMAR for the collection of the biological data and for sharing their datasets.

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VII. SUPPLEMENTARY MATERIAL

Table VII. 1. statistical analysis results: pairwise comparison of the reproductive outputs of species sharing nesting grounds. Note. R. output = reproductive output; LO = olive ridley; CC = loggerhead; EI = hawksbill; DC = leatherback.

Location	**Species compared**	**R. output**	**Levene**	**Wilcoxon**
Pirambu - SE	CC / LO	HS	**0.05634**	< 2.2e-16
		ER	< 2.2e-16	< 2.2e-16
Busca Vida - BA	CC / EI	HS	7.82e-05	< 2.2e-16
		ER	0.003135	< 2.2e-16
Comboios - ES	CC / DC	HS	**0.8186**	2.657e-06
		ER	**0.719**	0.01237

Table VII. 2. pairwise comparison results for local climate predictors between the three locations. p-value adjustment method: Bonferroni.

Climate variable	**Pirambu vs. Busca Vida**	**Pirambu vs. Comboios**	**Busca vs. Comboios**
Sand	**1**	1.52201e-06	5.141674e-04
Air	9.1e-05	2.9e-11	0.0014
Humidity	6.2e-15	1.3e-11	**0.079**
Rainfall	**0.21997**	**0.14697**	0.00021

Table VII. 3. nests included in the GAM analyses – locations, species and number of months studied do not differ from the previous analysis, but certain nests had to be excluded before running the models due to a lack of consistent climate data available.

State	**Location**	**Species**	**Number of nests**
Bahia	Busca Vida	*Loggerhead* *Hawksbill*	433 77
Espirito Santo	Comboios	*Loggerhead* *Leatherback*	1,284 88
Sergipe	Pirambu	*Loggerhead* *Olive Ridley*	233 2,457

Table VII. 4. Occurrences of the different temporal scales of the 4 climate predictors (mean air temperature, sand temperature, accumulated rainfall and mean humidity) in all the best overall GAMs. CC = loggerhead; LO = olive ridley; EI = hawksbill; DC = leatherback.

Variable	**Parameter**	**1.2**	**lay-2**	**lay-1**	**lay**	**inc**	**hatch**
CC Pirambu	HS	-	-	-	2	1	1
	ER	-	-	1	2	-	1
LO Pirambu	HS	-	-	2	-	-	2
	ER	-	-	1	-	2	1
CC Busca Vida	HS	-	-	1	1	1	1
	ER	-	-	2	1	1	-
EI Busca Vida	HS	-	-	-	-	4	-
	ER	-	-	2	-	2	-
CC Comboios	HS	-	-	-	-	3	1
	ER	-	-	-	-	3	1
DC Comboios	HS	-	-	1	-	-	3
	ER	-	-	-	-	4	-
Total	HS	**0**	**0**	**3**	**3**	**9**	**9**
	ER	**0**	**0**	**6**	**3**	**12**	**3**

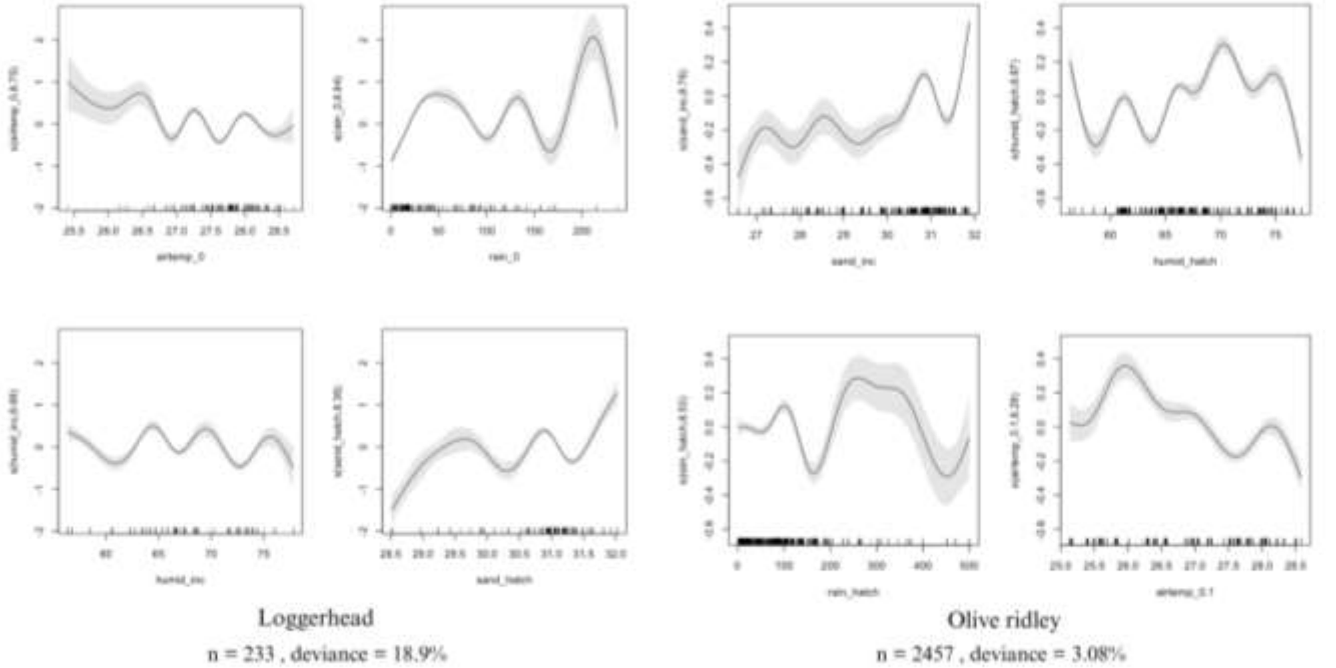


Figure VII. 1. Best predictors of hatching success at Pirambu beach, Sergipe.

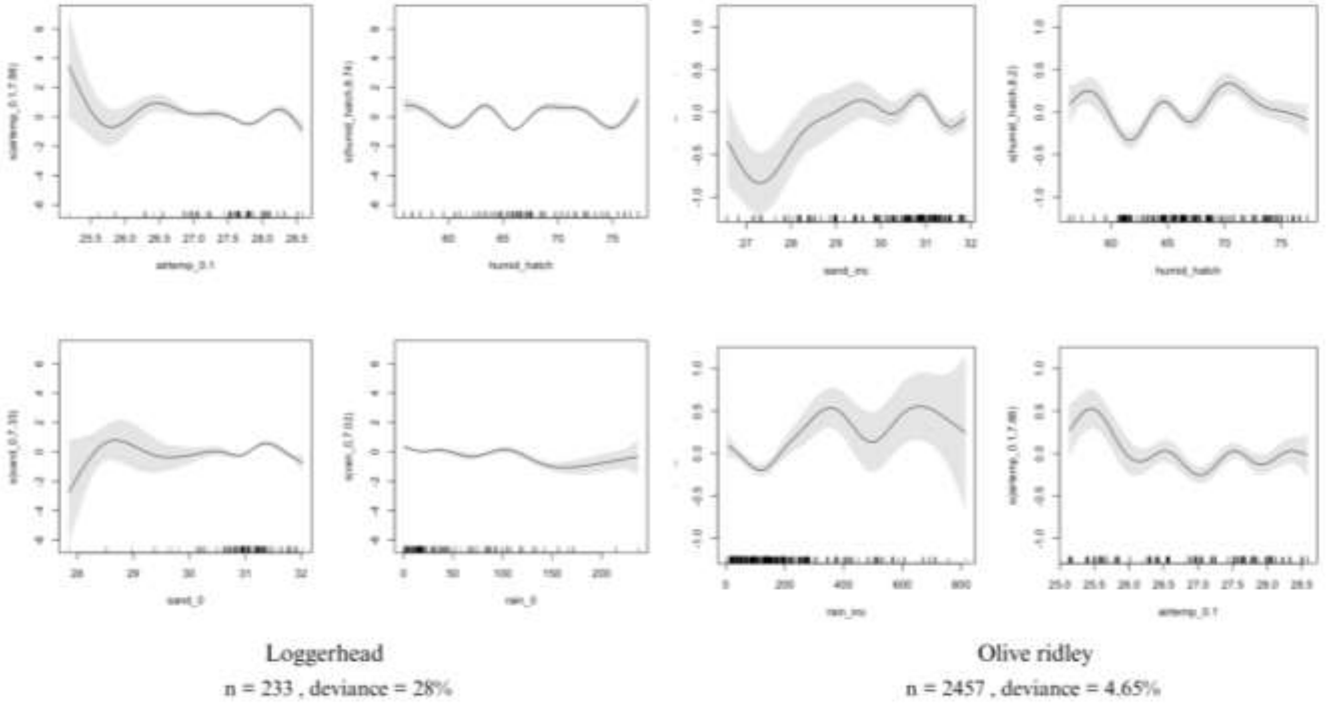
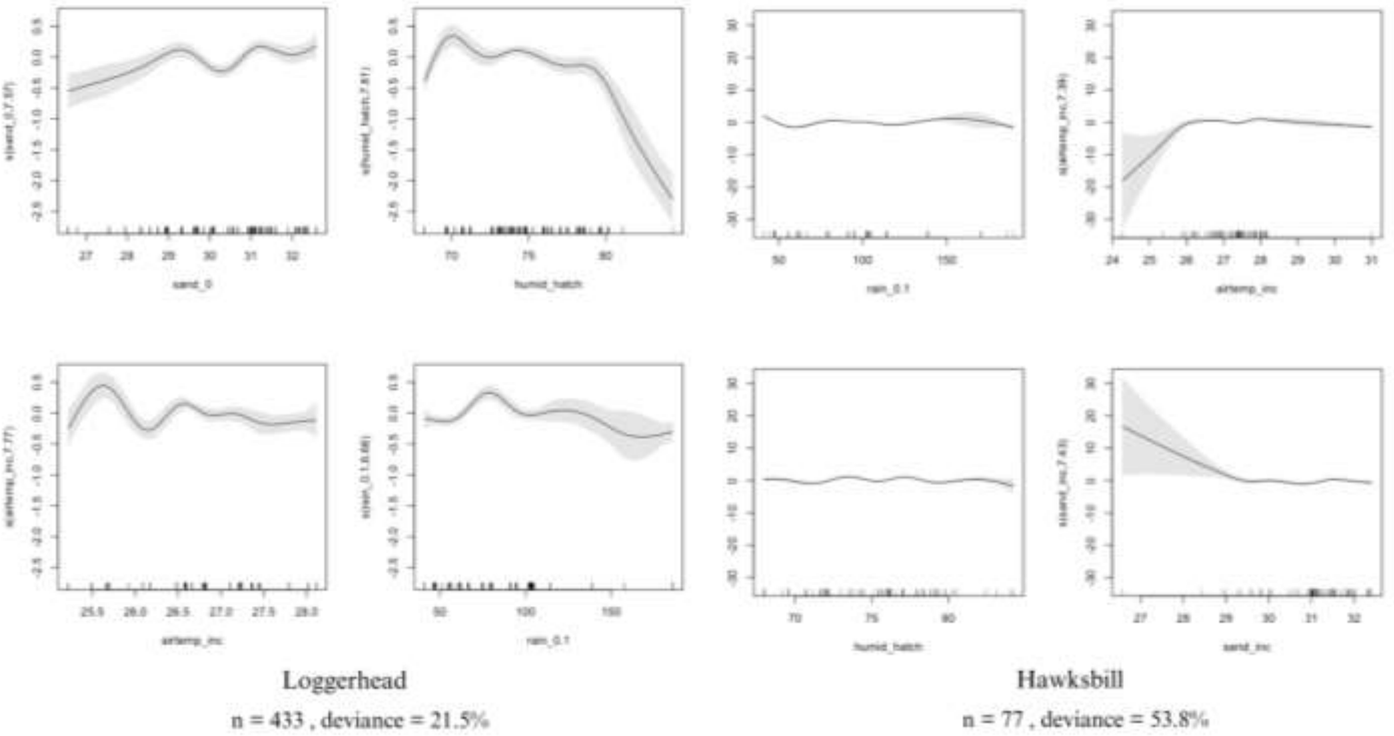


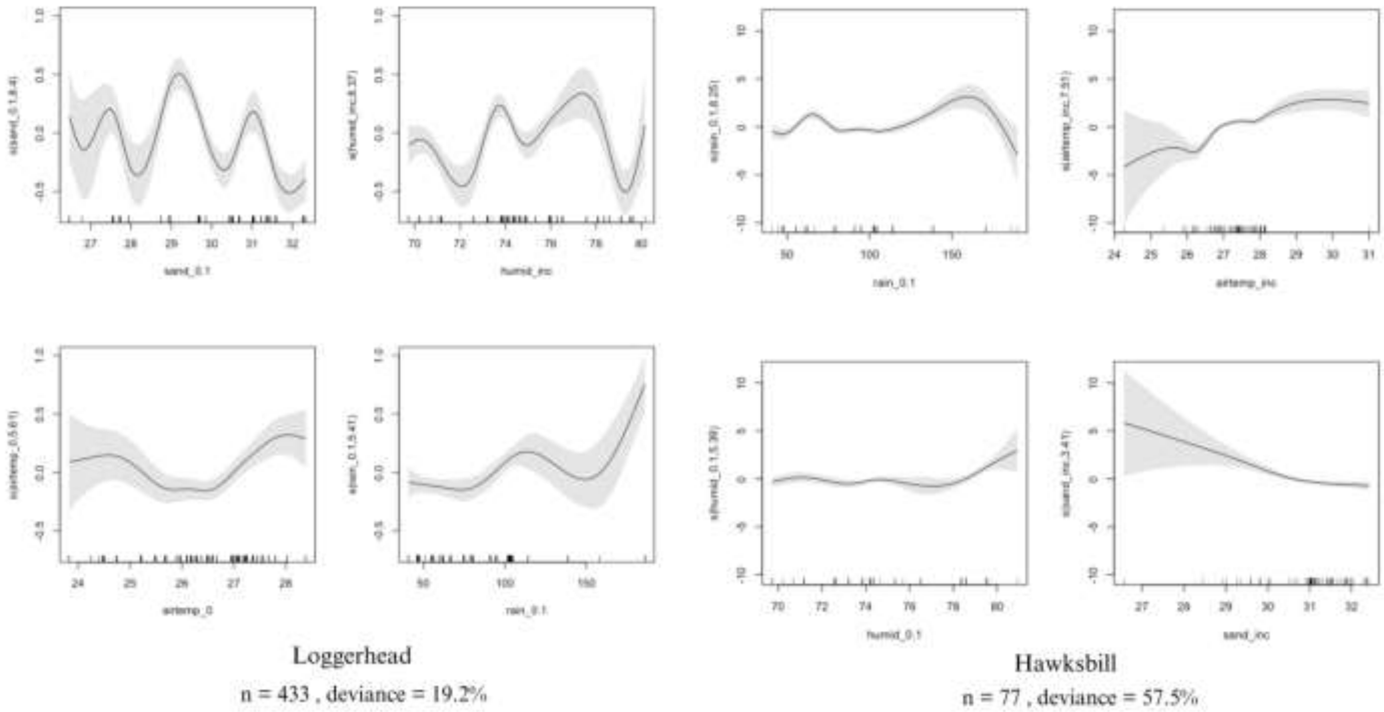
Figure VII. 2. Best predictors of emergence rates at Pirambu beach, Sergipe.



Loggerhead
n = 433 , deviance = 21.5%

Hawksbill
n = 77 , deviance = 53.8%

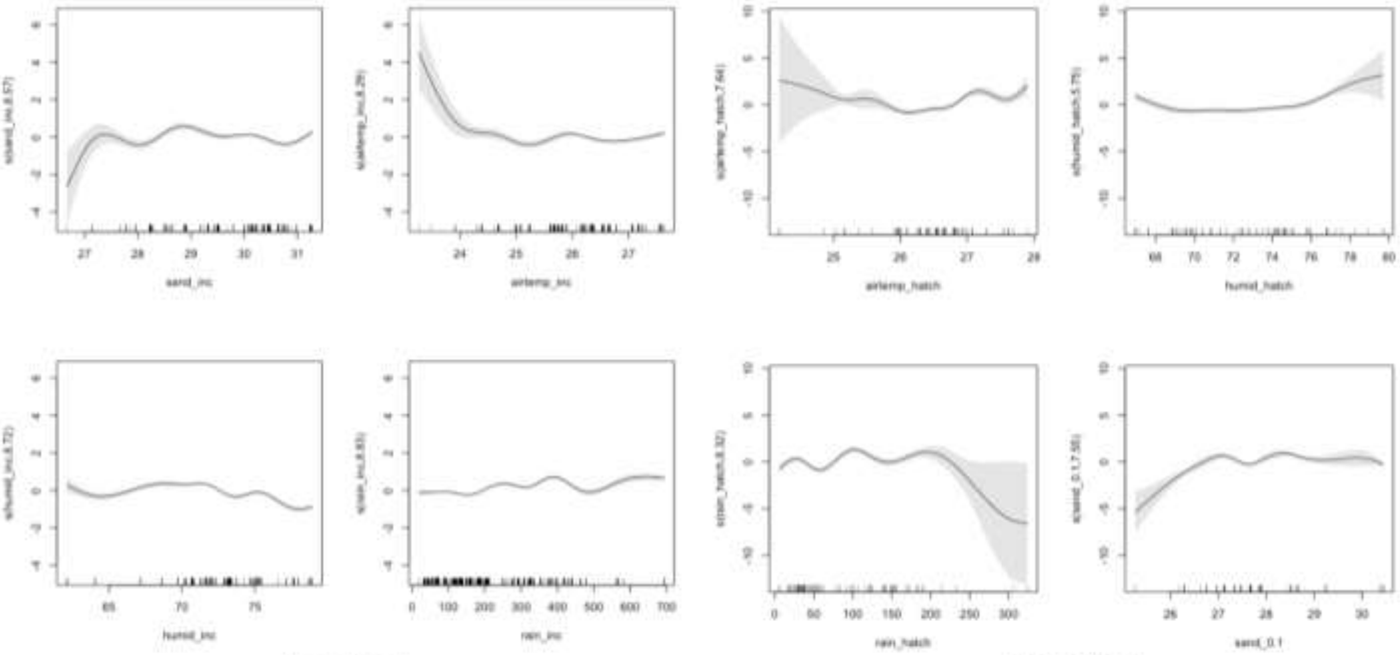
Figure VII. 3. Best predictors of hatching success at Busca Vida beach, Bahia.



Loggerhead
n = 433 , deviance = 19.2%

Hawksbill
n = 77 , deviance = 57.5%

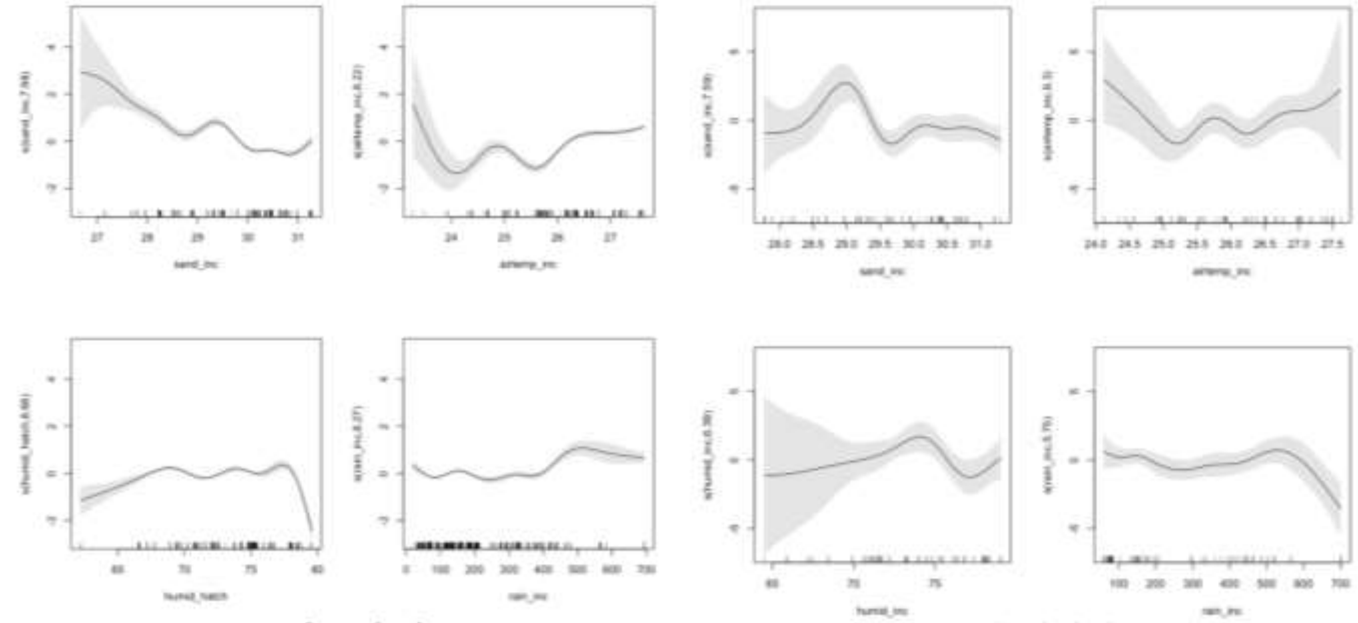
Figure VII. 4. Best predictors of emergence rate at Busca Vida beach, Bahia.



Loggerhead
n = 1284 , deviance = 6.53%

Leatherback
n = 88, deviance = 52.9%

Figure VII. 5. Best predictors of hatching success at Comboios beach, Espirito Santo.



Loggerhead
n = 1284 , deviance = 10.1%

Leatherback
n = 77, deviance = 51.6%

Figure VII. 6. Best predictors of emergence rate at Comboios beach, Espirito Santo.

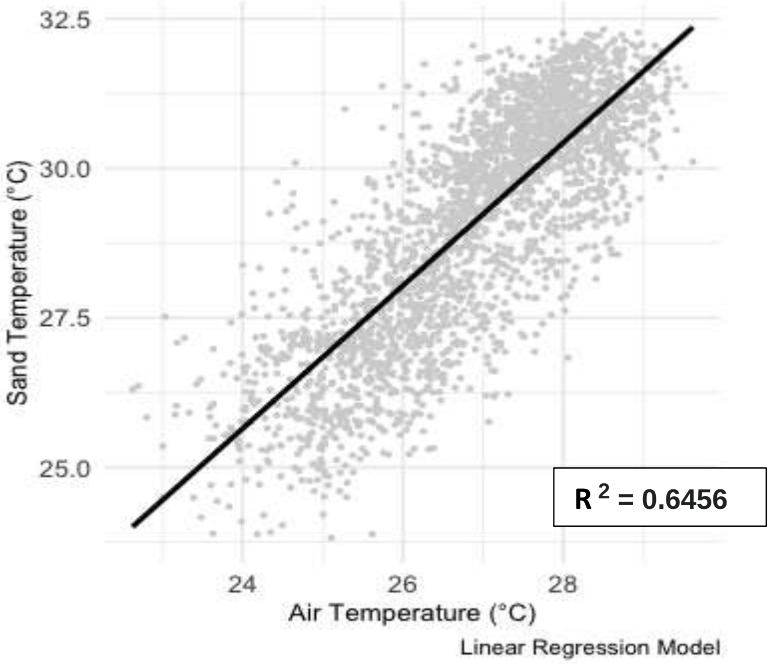


Figure VII. 7. Correlations between sand and air temperature at Pirambu beach, Sergipe, between October 2013 and December 2020.

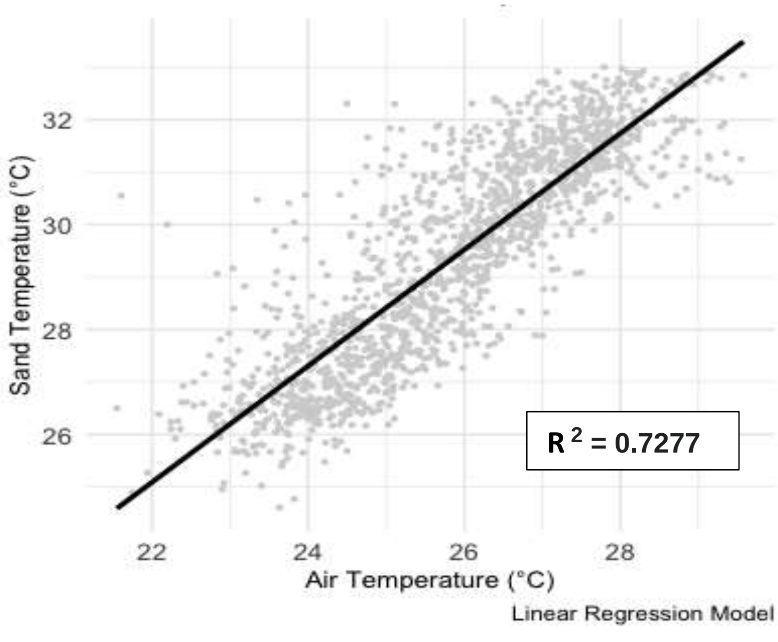


Figure VII. 8. Correlations between sand and air temperature at Busca Vida beach, Bahia between October 2013 and December 2020.

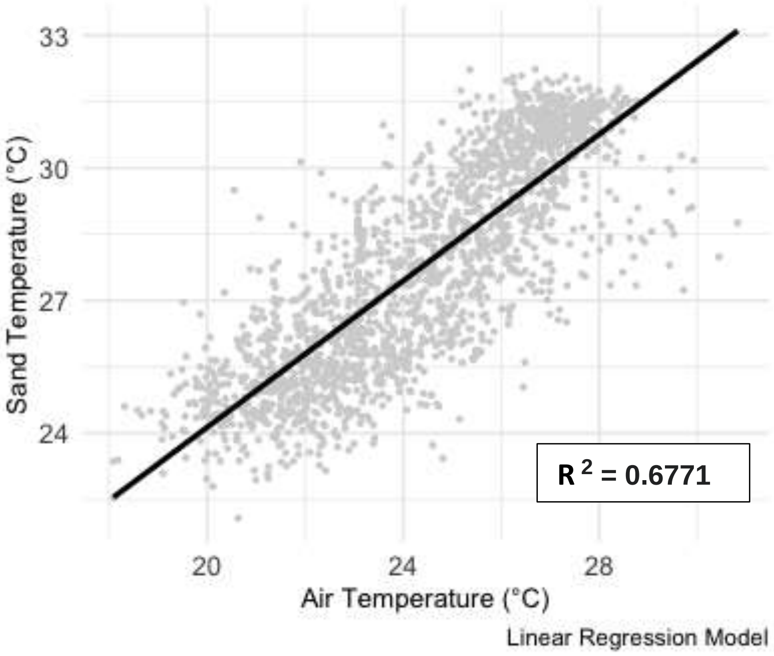


Figure VII. 9. Correlation between sand and air temperature at Comboios beach, Espirito Santo between October 2013 and December 2020.