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Sea Turtle Nesting: What Is Known and What Are the Challenges under a Changing Climate Scenario

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Abstract

The rate of climate change experienced globally in recent decades may compromise sea turtles' survival; especially temperature increase, which is particularly fast, impacts life history characteristics, such as temperature-dependent sex determination (TSD), late maturity and sea turtles highly migratory nature. This review aims to identify and summarize the information that has been collected from 2009-2020 in order to aid future empirical studies that seek to fill these and other knowledge gaps, and subsequently assist conservationists in making multilevel decisions to protect sea turtle populations and species. In a summarized way the general knowledge acquired so far on the influence of environmental abiotic and biotic factors on nesting behaviour and hatching, emergence and survival successes of sea turtle hatchlings, was gathered. To accomplish this work, a search on Web of Science, Science Direct, NCBI/PubMed, and Google Scholar was carried out using the terms "sea turtles + climate change". Published articles in the period 2009-2020 were selected, related to the nesting ecology of 5 species of sea turtles: *Caretta caretta*, *Eretmochelys imbricata*, *Dermochelys coriacea*, *Chelonia mydas*, *Lepidochelys olivacea*. Emphasis was also placed on geographical information and on population location (e.g. climatic conditions during the nesting season). These articles (N = 126) were analysed giving relevance to researcher's data interpretations, comparisons with other researches, and the reached conclusions. An attempt was made to represent all 5 species of sea turtles when selecting articles on each of the environmental factors that influence sea turtle nesting: temperature, humidity, nesting substrate, gases, depth of the nest, sea surface temperature (SST), nest location on the beach, nesting phenology and geographic distribution of nesting habitats. The interaction between these parameters and their consequences on the terrestrial phase of reproduction are presented and discussed.

Keywords

Reproductive Ecology, Sea Turtles, Climate Change, Nesting Phenology and Geographic Distribution of Nesting Habitats

1. Introduction

The oldest fossil of sea turtles dates back to more than 120 million years, belonging, a species described under the name of *Desmatochelys padillai*, a vast group were dermochelyids, and cheloniids are included [1]. Despite the showed capacity for adaptation and survival to various climate changes [2], the rate of climate change experienced globally in recent decades, especially temperature increase, is particularly fast, so life history characteristics of sea turtles, such as temperature-dependent sex determination (TSD), late maturity and highly migratory nature may compromise their survival [3] [4]. Habitat destruction, persecution and other direct anthropogenic pressures contribute to sea turtles being particularly vulnerable animals to climate change [5].

Current changes in climate manifest themselves mainly through the unprecedented warming of air temperature but also changes associated with the ocean-atmosphere system [4]. Examples of these changes are irregularities in precipitation patterns [6] [7] and the increased intensity and frequency of cyclonic events and storms [8] [9]; sea-level rise (SLR); changes in ocean salinity and pH [10]. Their interconnection and the effect of changes in synergy are even more complex to study.

Species whose life strategies are closely linked to the climate, such as sea turtles and other ectothermic living creatures [11] [12], will be vulnerable as changes may act as insurmountable evolutionary barriers [13]. Sea turtles have a "complex life cycle where the adult and embryonic stages have different habitat requirements and physiological tolerances to environmental conditions" [14]. By being vulnerable to the effects of climate change in both terrestrial and marine habitats, predicting the potential impacts of climate change on population persistence becomes challenging [15].

The scientific community's efforts to curb these effects involve, for example, protecting both territories. Almost 80% of protected areas (PAs) containing nesting sites are classified as marine protected areas (MPAs) [15] and contain sea turtles, or their coastal habitats, tending mainly towards the protection of breeding habitats [16]. However, Scott *et al.* [16] consider that, compared with other coastal systems such as coral reefs and mangroves, sea grass meadows function as refuges and feeding habitats for turtles are poorly represented in MPAs.

Additionally, while protected areas are static, the populations and abiotic factors that characterise them are dynamic, spatially and temporally [5], which may lead to the redefinition of their boundaries. It is necessary to assess whether these protected areas continue to match population preferences and predict whether they will do so in the future, in order to conserve not only nesting beaches, but also migratory corridors [5] and feeding areas, or to redefine them; to this end, advances in tracking technologies will be of paramount importance [16].

Additionally, much of the biological processes of sea turtles that take place in the marine environment are still poorly understood [17]. It becomes difficult to predict how climate change might affect them in the aquatic environment and to design conservation measures accordingly. Therefore, to date, mitigation techniques for the predicted decline in sea turtle populations are directed particularly towards trying to ensure that nesting habitat is available now and, in the future [18], preventing females from nesting in sub-optimal habitats.

In this review, the effects of individual characteristics and environmental factors on the incubation of sea turtle eggs, in general, are summarised. The interaction between these parameters and their consequences on the terrestrial phase of reproduction is discussed on the basis of studies carried out between 2009-2020; changes in the aforementioned parameters or their interaction caused by climate change, that have already been detected, or that are predicted, are presented and discussed. Finally, gaps in knowledge, aspects that remain under debate and methodological difficulties identified by previous research are identified.

2. Method

A search on Web of Science was carried out using the terms "sea turtles + climate change" in the period 2009-2020. Documents that related to the nesting ecology of 5 species of sea turtles were selected: *Caretta caretta*, *Eretmochelys imbricata*, *Dermochelys coriacea*, *Chelonia mydas*, *Lepidochelys olivacea*. Emphasis was also placed on information on geographical and population location (e.g. climatic conditions during the nesting season). Information related to species, location and time of year as well as environmental characteristics of nesting beaches (some even in close proximity) and the diverse responses of populations of a single species was organized taking into account the effects of various environmental factors on various aspects of sea turtle nesting, namely on maternal characteristics (e.g., nesting site selection, egg yolk supply) and environmental characteristics (e.g., temperature, albedo, oxygen, humidity, soil type, salinity, presence of microorganisms), both in space (e.g., within the beach, between beaches, at feeding sites) and in time (e.g. start and duration of the nesting season, remigration intervals). Further research on each of these parameters was carried out using more platforms (e.g., Science Direct, NCBI/PubMed, Google Scholar).

In the synthesis, it was sought to highlight which climatic factors and how they influenced those parameters, and in turn, how they influenced nesting and egg incubation and what effects they had on the survival of the hatchlings, which would later become the new breeders. It was also tried to expose the impacts of climate change on these parameters and what are the implications (already detected or predicted) in the nesting of sea turtles and incubation of their eggs. Because there is an interaction between these factors and it is not possible to discriminate the effect of each one, a joint analysis was made within each specific topic.

The topics that still remain understudied are also referred to and the questions whose answer is not consensual, namely those related to the responses of the detected/predicted populations being phenotypic or adaptive changes. A discussion is held on the basis of published work, not only on sea turtles but also on other reptiles, and related content (e.g., variation in the norm of thermal reaction) as well as on the physiology of the species or populations (e.g., Transitional Range Temperature (TRT), pivotal temperature) and on the effect of environmental conditions on the physiology but also on the incubation conditions themselves (e.g., effect of nest microclimate temperature on incubation duration).

3. Results of the Review and Discussion

Documents, mostly papers, from 2009-2020 on each of the abiotic parameters, temperature, humidity, soil type, gases and microorganisms were sought to give a general idea of what was known so far and to provide a framework on each topic. From the range found, those related to climate change were selected and many of them were selected as case studies to support ideas and conclusions throughout the text. The same procedure was followed for biotic parameters, related to the life history and biology of sea turtles, microorganisms, as well as the nesting and incubation processes themselves. It was always intended to find studies done *in situ* and artificially for each of the topics. Finally, we tried to find out how the climate had varied in the locations discussed throughout the text and to put climate projections for each location as updated as possible, preferring the most recent articles. The knowledge gaps identified by the researchers, especially in more recent articles, were always identified and saved. Has a result, 126 references were selected which contribute for each topic. It should be noted that some articles (N = 12) outside the 2009-2020 range were used to further clarify specific aspects of sea turtle nesting biology, terms on their ecology (e.g. thermal reaction norm) or climate/climate change aspects.

3.1. The Temperature

The study of the effects of temperature on sea turtles is the subject of numerous studies. Like other reptiles, they are ectothermic. Furthermore, the sexual determination of their hatchlings is temperature-dependent, this being an example of **phenotypic plasticity**. More recent studies on the effects of temperature on incubation have focused on the responses of embryos at different stages to different variations in incubation temperature. The more refined the understanding of embryo response, the better predictions can be made under a global warming scenario.

The pivotal temperature, the constant temperature at which both sexes are produced at the same proportion [19] and, if different the ratio becomes biased in favour of the production of the other gender [20]. It is not known what is the magnitude, nor at what rate the imbalance of sex ratios may occur in the expected climatic framework.

The **pivotal temperature** of each species has been determined by experimental method, being inserted in the transitional temperature range (TRT) limits and up to the thermal tolerance limits (minimum and maximum) only one of the sexes is produced [20]. In order to **calculate sex ratios in the nest**, the pivotal temperature is often assumed to be the average temperature during the **thermo sensitive period** (TSP) [21].

Lolavar & Wyneken [20] **have shown** that the moisture content of the sand plays a significant role in **determining the TRT** and thus the sexualisation response of embryos to temperature.

These studies (on pivotal temperature and TRT) are generally based on controlled experimental studies, which do not realistically reproduce the fluctuating and dynamic conditions that embryos are subjected to during *in situ* incubation [20] [22]. Therefore, more and more studies seek to include these fluctuations and their relationship in order to produce an experimental environment that more closely resembles the nest microenvironment and to use models that include more variables to obtain closer values to those found *in situ*.

Knowledge of these parameters in the framework of climate change tells us that populations with a broad TRT may continue to produce both sexes, despite the increase in atmospheric temperature, suggesting greater resilience [21]; the percentage of females produced will increase and therefore the potential future fecundity as well, possibly mitigating the negative effects of high atmospheric temperature on population size [23]. However, the extent to which reproductive traits like TSD will function as adaptive mechanisms is not known, nor whether they may constitute a viable solution against population decline.

Nests are therefore vulnerable to temperature variation and multiple factors make the temperature vary during incubation. Some factors are related to the female and the clutch (the place where she deposits the nest on the beach, the moment in the nesting season, excavated depth, clutch size), and others are related to the edaphoclimatic factors (*i.e.* air and sand temperature, humidity, type of substrate, shade). The combination of these factors, which entails variations in incubation temperature, leads to the formation of incubation "microenvironments". Considering this aspect, some researchers speak about the **existence of refuges** that are favourable to male incubation (*i.e.* lower temperatures) such as, for example, the periphery and bottom of the nest, in the vegetation lines [21] [24] and intertidal zone of the beach and on beaches with a light-coloured substrate, these being of a spatial nature [21]; and the cooler periods of the nesting seasons can be considered as temporal microrefugia, favourable for male incubation.

Mortality and Incubation—Given the thermosensitivity of embryos, as nest temperature approaches the thermal tolerance limit (where embryonic development and hatching still takes place), embryonic mortality increases and hatching success decreases [25]. Authors such as Bladow & Milton [26], among others, have reported substantial reductions in hatching success in sea turtle nurseries related to very high nest temperatures.

Kobayashi *et al.* [27] found that high incubation temperatures appeared to lead to a greater increase in early-stage mortality; they then suggested that it is at this stage of development that embryos are most sensitive to high temperatures. Recently, Sifuentes-Romero and co-authors [28] reported that it is during histogenesis to organogenesis, *i.e.* also at the beginning of incubation, that embryos appear to be most sensitive to temperature and that thereafter, it is not temperature but the humidity that has the greatest impact on embryo development. Bladow & Milton [26], on the other hand, do not reveal a significant difference in the sensitivity of the different stages to elevated temperatures.

The increase in mortality seems to be more expressive when embryos are exposed more frequently, and for longer periods, to elevated temperatures; thus, embryos have some tolerance to temperature [14]. This thermal tolerance varies between species and between populations, which translates into **"phenotypic plasticity"**. This finding explains that the overall extent of embryonic mortality varies. For example, Tomillo *et al.* [13] found that the hatching success of *Dermochelys coriacea* decreases from 30˚C, while that of *Chelonia mydas* and *Lepidochelys olivacea* only decline from 32˚C. Therefore, very high nest temperatures have a greater negative impact on leatherback turtles, as lower temperatures can cause nest mortality. This fact contributes to their hatching success being lower than that of green turtles and olive ridley turtles [13].

Tedeschi *et al.* [29] found that, under high incubation temperatures, embryos increased the transcription of genes encoding heat shock proteins (Hsp's), known to alleviate several negative effects caused by high temperatures on metabolic processes. In this study, *Caretta caretta* embryos incubated in nests with sub-lethal temperatures showed a positive regulation of Hsp70 and Hsp90 mRNA in cardiac and brain tissues; they also revealed that hatching success was similar to that of controls. As a heat stress response was produced without causing mortality, Tedeschi *et al.* [29] presented the genes of these Hsp's as appropriate biomarkers to measure the thermotolerance response of embryos.

This study shows that a better understanding of heat stress response mechanisms (molecular, cellular and physiological) will be useful in predicting the resilience of embryos to increased incubation temperatures resulting from climate change.

Incubation, gender, size and abnormalities. The temperature inside the nest increases throughout incubation due to the substantial increment in metabolic heat generated by eggs, caused by the acceleration of metabolism during embryonic development [30].

Incubation duration is determined by the rate at which embryos develop, so if environmental conditions make the nest ambient temperature itself high, adding the contribution of metabolic heat [31] [32], the developmental rate will be very high, shortening the egg incubation period [29]. In this situation, nest temperatures more easily exceed the pivotal temperature, causing, in parallel with the shortening of the incubation period, the proportion of female offspring to increase. This is the reason why it is often assumed that in nests where the incubation duration is shorter, a higher percentage of females is produced [33].

This assumption has been used in many studies, like dei Marcovaldi *et al.* [34] and Calderon-Peña *et al.* [35], to predict sex ratios within the nest because until now the only way to check the sex of the hatchlings was by performing a laparoscopy or histological analysis. This involves the sacrifice of live hatchlings and therefore entails at least ethical and logistical complications [36]. Recently, Tezak *et al.* [37] presented a new technique to identify the sex of hatchling turtles using small blood samples.

High temperatures during incubation can also lead to the production of hatchlings with morphological abnormalities. For instance, in the carapace, if they occur during the mid-developmental stage [38], but also at the physiological and cellular level; for example, Fleming *et al.* [39] detected through blood analysis a change in hemodynamic balance (dehydration) and potential inflammation and/or stress in hatchlings emerging from nests that incubated at elevated temperatures. However, the effects of temperature, as well as other environmental factors, on various aspects of the physiology and morphology of sea turtle hatchlings need further study.

Several studies have found that hatchlings incubated in warm nests are smaller compared to those from cooler nests with temperatures in the optimum temperature range, although there are no significant differences in hatchling mass [31]. In embryos incubated in nests with high temperatures, the rate of embryonic development is so high that a substantial part of the yolk does not get converted into tissue before hatching [24] [31] [40] [41] becoming smaller; the increase in hatchling size implies a smaller proportion of remaining yolk and a slower/colder incubation [24] [41].

Müller, Ruiz-García, García-Gasca & Abreu-Grobois [42] reported that lower than optimal intermediate temperatures lead to slower development and simultaneously smaller offspring, thus the balance between temperature and speed of development described above does not apply. These researchers, therefore, suggest that not only under very high temperatures but under any non-ideal temperature regimes, the organism prioritises survival over growth, with other physiological processes also being involved.

Sifuentes-Romero and co-authors [28] suggested that embryos are most sensitive to temperature during histogenesis and organogenesis, and that this can produce permanent effects on the phenotype of the offspring (e.g. sex), but when the embryo starts to increase body size it is the availability of water, to support the rates of metabolism and growth, that has the greatest impact on development.

Despite the above studies, there are still few studies that focus on the analysis of the degree of influence of the variation of a given environmental factor on incubation. Increased knowledge about the effect of these factors on embryonic development, individually and in conjunction with others, at a cellular, physiological and morphological level may help clarify several hypotheses. The 'thermal reaction norm' (where the TSD response is included [19]) implies that body size decreases with the increasing temperature at which individuals incubate [40] [43] [44].

Hatchling performance and post-hatch survival—Several studies have analysed the consequences of hatchling's phenotype on their survival, particularly concerning body size [40]. This parameter is often used as a hatchling quality indicator, as it is determinant in life's history transition: from nesting beaches to the oceanic stage [45]. It should be noted that the **maternal factor** (egg yolk proportion) also conditions the size of the hatchlings: according to the Dynamic Energy Budget (DEB) model, the feeding conditions of the female parent affects the density of reserves that she can provide to the hatchlings during vitellogenesis [46] and that are stored in the egg to be used for the formation of embryonic tissue throughout incubation. Patel *et al.* [47] suggested that **potential deterioration of feeding areas** resulting from changing marine environment conditions threatens hatching success [47] and leads to the production of hatchlings with a less advantageous phenotype (smaller body size) [46].

It has been reported that **larger hatchlings have better locomotor performance**, both on land [48] and in water (e.g. [31] [45]). This ability is critical for an effective response to the high predation rate to which hatchlings are subjected during the journey along the beach and across coastal waters to the safer open ocean [11]. In addition to speed, greater body size may allow hatchlings to avoid "gape-limited" predators that abound in shallow, near shore waters [49]. These predators cannot capture prey above a certain size, which is determined by the size of their own mouth; consequently, larger prey is favoured by selection [50]. Le Gouvello *et al.* [45] concluded that concerning offspring, sea turtles follow the hypothesis of 'the bigger the better'; *i.e.*, the larger offspring has the phenotype that maximizes survival, at least during an early life stage.

3.2. Humidity

With the course of climate change, the frequency, distribution and intensity of storms and cyclones are predicted to increase mainly in tropical regions [51] [52]. Although **precipitation is predicted to increase in some nesting regions**, in most of these areas **total precipitation is predicted to decrease** and, simultaneously, precipitation will become less frequent but more intense [52]. Erratic precipitation patterns are therefore predicted throughout the 21st century [7]

[52]. **Precipitation affects the nest microenvironment**, mainly through its role in temperature variation and moisture variation.

Extreme events will affect sea turtles in the **short-** and **long-term** (over several generations) [51] [52]. **Short-term** effects will directly affect the water content of the sand, either by rainwater or by seawater that floods beaches [53] when buffeted by wind (sea spray and waves) and will lead to extreme tidal variations and low barometric pressures that discourage nesting activity [8], increasing mortality within the nests [53]. **They will also entail further coastal erosion, reducing in time the available area for nesting at a given site, and to its possible abandonment.**

Several studies report a cooling effect on nest incubation by precipitation. Cooling has greater expression in the upper layers of the nest compared to the deeper layers [54] because these are originally less humid and therefore subject to greater temperature fluctuations. Consequently, precipitation can increase the incubation period and favour male production within the nest [33] [55], but only if precipitation events are prolonged. That way they may provide **cooling periods long** enough to coincide with the TSP [54]. Otherwise, the tendency of nest feminization may persist even if it rains, as Lolavar & Wyneken [54] report in their study.

Durable cooling in sand temperatures is achieved when under prolonged precipitation the cloud cover, by preventing some of the solar radiation from reaching the beach, keeps the cold rainwater cooling the sand [54] [56]. In contrast, inconsistent precipitation events cause poor cooling because as soon as it stops raining, the sun warms the surface sand layers and some of the heat, which is not dissipated in or by water evaporation, can be conducted to lower nest layers [57]. Thus, the **increase in sand moisture** provided by rainfall is not always advantageous for incubating eggs. On the one hand, precipitation can provide water levels necessary for successful embryonic development [58]. But several studies report evidence of a **negative effect of humidity** on hatching success and hatchling emergence [12] [59]. This is because, as already mentioned, it can potentiate an increase in mortality within the nest, in phenomena of "egg boiling", egg asphyxiation (by **hypoxia conditions**, due to direct water saturation of the soil) or even **egg dehydration** (due to direct soil saturation, especially when eggs are surrounded by saltwater, or the rising water level of the groundwater table) if the water potential is so high that it does not allow eggs to maintain the amount of necessary water for their development [59].

Lolavar & Wyneken [20] demonstrated that sand moisture provided by rainfall plays a **significant role in determining TRT** (transitional range of temperature). **Under extremely low or high moisture conditions**, the range of TRT becomes narrower; therefore, fluctuating moisture conditions may contribute to the sex ratios variability within the beach and throughout the nesting season.

The **effects of precipitation on hatching success are not uniform on a global scale** [56]. In sites with prolonged droughts/low average precipitation, continuous precipitation events generally have a positive effect, compensating for thermal and water stresses typical of hot and dry sites [56]. However, very high levels of precipitation could result in increased egg and hatchling mortality [60].

In naturally wetter locations or in temperate climates, extreme events of prolonged precipitation, such as storms, will exacerbate the negative effects caused by moisture, as they will easily cause it to cross the threshold supported by embryos and increase the likelihood of nest inundation by groundwater tables and thus the mortality rate [61]. In addition, these extreme high rainfall events contribute to lower nesting activity [8] and decreased reproductive output, especially if they occur during peak seasonal nesting [61].

3.3. Nesting Substrate

The properties of the sediments that make up the beach substrate are a function of the interaction between the geological structure of the area and environmental variables. The physical and chemical characteristics of the nest substrate strongly condition incubation, and within the relatively little information published to date, the best documented are mineral composition, albedo and grain size.

Sediment Type and Size

Substrate properties appear to influence nesting females' behaviour. When female attempts to nest on a muddy substrate, crawling becomes more difficult, potentially leading to animal exhaustion and its death; still, many turtles nest in areas that have variable contents of fine-grained sediments [59].

In the literature, it is reported that **larger sand grains** offer greater porosity and therefore greater soil ventilation and lower salt content, as this can be more effectively washed away by rainfall [62]. They thus present an overall positive effect on hatching success. On the other hand, they also present low water holding capacity providing a drier and warmer environment for the embryos, as well as hindering the rise of the hatchlings after hatching (higher probability of the nest collapsing) [63].

In contrast, Marco and co-authors [59] found that **eggs incubated on substrates rich in fine-grained sediments**, such as clay and silt, also suffer dehydration, as the low permeability, low drainage, provide high water retention, and generate a strong water potential that prevents water from flowing to the eggs. Mass loss (due to water loss) and consequent embryonic mortality increase with the proportion of shell in direct contact with the soil; *i.e.*, this is mainly seen in eggs from the periphery of the lay. In addition, the **high compaction characteristic of this type of sediment** may prevent the ascent of the hatchlings from the nest chamber to the beach surface and, in conjunction with a high-water retention capacity in the interstitial spaces, lead to poor gas exchange between the eggs and the environment outside the nest, impairing embryonic development. They also detected a reduction in locomotor performance in hatchlings whose embryonic development was impaired by the presence of these fine materials (silt/clay). In contrast, Saito and co-authors [63] observed higher hatching and emergence successes in hatchlings from nests established in a fine-grained substrate and better crawling and swimming performance and did not detect a greater effort by the hatchlings to ascend to the surface.

For example, while in sandy substrates nest depth regularly provides typically higher hatching success, in clay/silt-rich substrates success is higher in shallower nests, as in general these fine sediments are only present after a surface layer, thus having a lower proportion of clay/silt surrounding the nest chamber [59].

It should be noted that, like most studies on the effect of sediment on turtle incubation, the experiments were carried out under manipulated conditions, where the complex relationship between substrate characteristics and climatic conditions, nest location and nest depth can hardly be taken into account.

Increased knowledge of the sedimentological characteristics of nesting beaches and their effects on nesting and incubation is needed to understand how they affect the vulnerability of nesting beaches to climate change and predict what implications potential alteration of sediments or their characteristics will have on sea turtle reproduction [64].

A study on the influence of chemical-mineralogical composition on incubation may also be relevant in the future, also considering the expected increase in storm frequency and its impact on erosion on nesting beaches.

Albedo: Albedo **is the fraction of solar radiation reflected** by beach sand (*i.e.*, the albedo); it is a property **strongly influenced by sediment colour** [65]. The effects of this property on incubation are often studied by comparing nests established on light sand beaches, usually of biogenic origin, and dark sand beaches, normally of volcanic origin [66].

Dark sand has a lower albedo and therefore greater absorption of solar radiation. Consequently, dark sands have higher temperatures (and **higher mean temperature**) than light coloured sand beaches, translating into a significant difference in mean incubation temperatures [22] [66]. Therefore, for dark sand beaches, several studies report: 1) The more pronounced feminisation of nests established there compared to those on light sand beaches (e.g. [67]), also revealing a possible lack of *in situ* temperature-pivotal adaptation [22]; 2) A shorter incubation period; 3) Production of smaller hatchling sizes but higher yolk mass; 4) Lower hatching success. Weber *et al.* [66] collected eggs from two beaches (one with dark volcanic sand, the other with light biogenic sand) that therefore provided very different developmental environments but were only 6 km apart and subjected them separately to similar high incubation temperatures. However, it was found that the **damage caused by high temperatures was less marked in embryos from dark beaches** than in embryos from light sandy beaches and noted that the first ones have shallower thermal reaction standards, allowing them to suffer less marked changes in parameters previously mentioned. Still, high temperatures continued to be detrimental for these embryos, suggesting that embryos from dark sand beaches do not have a different thermal optimum than those from light sand beaches, but rather an expansion of the upper thermal tolerance limit. Finally, these researchers suggest that the higher heat tolerance of embryos from the dark sand beach is genetically based and reflects a local adaptation in this sea turtle population.

Studies such as that of Weber *et al.* [66], show that to some extent eggs incubated on dark sandy beaches suffer less drastic consequences than eggs from nests on light sandy beaches. However, the existence of such local adaptations to specific thermal conditions is not consensual. Tilley *et al.* [22] conducted a similar study in the same area, not finding evidence of fine-scale thermal adaptation. In any case, at several nesting sites, the temperature experienced by eggs is predicted to reach such high values in the near future that it will be difficult for potential "local thermal adaptations" to keep up with the temperature increase effectively.

In addition to colour, **thermal conductivity** affects the temperature of the nest environment; however, there are not many studies on this parameter. For example, Fadini *et al.* [68] found that although sand rich in biogenic sediments had lower albedo than quartz sand, it provided longer incubation periods for nests, due to the **low thermal conductivity** offered by biogenic sands, that enables **lower temperatures**. In this case, there was a reversal of the trend that nests located in sediment with lower albedo provided the highest temperatures, as the mineral composition of the sediments superseded the influence of albedo on temperature and consequently on incubation duration.

Other studies explore how certain parameters influence the substrate. The impact caused by **increased SST** and **ocean acidification** can influence the sediments that are transported to the beaches, in particular those of a carbonate nature, changing the sediment properties of nesting beaches [64]. Despite the recognized strong role of sedimentological characteristics in determining the nest microenvironment, there are not many studies about the effect of nesting habitat substrate on sea turtle reproduction.

Moreover, in nature, the beach substrate is actually a mixture of sediments, which may have different sizes and origins, and may vary in space, in-depth and horizontally, and according to weather conditions (e.g. storms and cyclones). So far, relations have been established between the grain size of the beach substrate and moisture, salinity, temperature, and gas exchange in the nest; as for the mineralogy itself, the main relation with the nest environment is through temperature, depending on the albedo capacity and thermal conductivity typical of each sediment type.

3.4. The Influence of Gases

During embryonic development the eggs release carbon dioxide, water (before hatching) and heat, and consume oxygen; hence the availability of oxygen is essential for successful incubation. These gas exchanges take place both between the clutch and the environment outside the nest and between eggs from the same clutch.

Inside the nest, the rate at which gas exchange occurs fluctuates throughout incubation, due to the variation in embryonic metabolism and the consequent increase in temperature.

According to Chen *et al.* [30], in the **early stage**, changes in oxygen content are subtle, due to the low rate of development. In the **intermediate stage,** on the contrary, the growth rate is rapid and, consequently, an increase in oxygen consumption by the eggs occurs, causing its concentration inside the nest to decrease, while the inflow rate is maximised. Finally, the rapid rate of development, characteristic of the **last stage** of incubation, allied to the increased activity inside the nest (the hatchlings break the eggshells and start the ascension path to the beach surface), lead to **even more expressive oxygen consumption** [30].

On one hand, these parameters (temperature, oxygen) act as the main reasons for the negative relation between posture size and hatching success, as detected in the study by I-Jiunn *et al.* [69]; on the other hand, a positive correlation between posture size and emergence success has been proposed. This is because larger groups of hatchlings emerging provide a lower energy cost per individual in ascending to the surface [70].

As there is a pronounced gas partial pressure gradient between the centre and periphery of the clutch and between it and the beach around the nest, the position the egg occupies within the nest will condition the amount of oxygen available to it during incubation [71]. Chen *et al.* [30] **found that oxygen content was indeed higher at the periphery** of the nest relative to the centre, as egg contact with the surrounding sands may facilitate gas exchange between the shell and the external environment.

Gas exchanges between the clutch and the surrounding environment are conditioned by factors such as humidity. Moisture can impair oxygen diffusion, because the higher the % occupancy of the pores by water, the lower the possibility of air circulation in these interstices, repressing gas exchanges between eggs and the environment [30]. This situation is more likely in nests established in places prone to flooding and in substrates rich in fine-grained sediments, which besides having a high-water retention capacity, have a high degree of compaction. It is important to note that **microorganisms** often present in nests can **consume a relevant amount of oxygen** during the decomposition of organic material, increasing the total oxygen consumption in the nest [72].

3.5. Microorganisms

Microorganisms exert an important selective pressure on oviparous animals, in so far as they can either facilitate or impede egg development. Microorganisms already identified in sea turtle nests are bacteria [73] [74] [75] and fungi [74] [75] [76] and generally have negative effects on incubation.

Gifari, Eldidasari and Sugoro [75] suggest that **microorganisms** can be transmitted from the female parent to the clutch during oviposition through the mucus of the cloaca and that contamination of this mucus is caused by the digestive condition of the female.

To date, the pathogenic microorganisms considered most common and with effects on the reproductive output, are some species of fungi of the genus *Fusa-*

rium, which are distributed in the main nesting areas of almost all sea turtle species [77]. **Fungi are transmitted from the sand around the nest** to the eggs on the periphery, which are in contact with the sand, then colonise the rest [77]. Their growth and spread are conditioned by changes in environmental conditions, in particular, temperature and humidity [78]. **Moisture** favours fungal proliferation, so nests established in sites more prone to tidal flooding or with silt/clay substrate are more susceptible to fungal invasion and, consequently, to having higher embryonic mortality rates, as Sarmiento-Ramírez *et al.* [77] found. On the other hand, the washing of the substrate by the tides decreases the amount of organic matter and microorganisms present in the sand [79]. This implies greater oxygen availability for the clutch, as it reduces oxygen consumption by microorganisms during the decomposition of organic material, increasing hatching success [72].

Situations that **imply a high content of organic material** around the nest then favour the proliferation of microorganisms that are pathogenic for the embryos. For example, the proximity between nests as a consequence of reduction of the nesting area, caused by SLR and human development, may have a similar effect to that of "arribadas". During these mass nesting events, the high density of postures promotes the accumulation of microorganisms in the sand, mainly bacteria, due to the high organic matter content derived from broken eggs during nest overlapping [79] and probably from the high amount of mucus deposited by females.

Moreover, regarding **fungi**, several species have an optimal growth temperature coincident with the optimal incubation temperature of sea turtle eggs [77]. This means that the optimal thermal conditions for egg incubation may also provide favourable conditions for growth and possible colonisation of the clutch by pathogenic microorganisms. Other species may also appear for the first time in places where, thanks to climate change, they have started to find favourable conditions.

Thus, the **modification of environmental conditions on nesting beaches** has implications not only for the embryonic development of eggs but also for colonisation and the emergence of pathogenic species that interfere with incubation [77], with possible devastating implications. Tsiafoulis, Dimitriadis, Boutsis and Mazaris [80] consider the **nematode community** present in nests as excellent **indicators of the ecological/functional** status of sea turtle nests. Their **diversity and taxonomic richness** are closely associated with the **increased hatching success** of the hatchlings. They suggest that further exploration of this information may provide new techniques to monitor nest incubation and to find techniques to protect incubation areas.

Also, Hoh, Lin, Sidique and Tsai [76] found significant differences between the **sand microbiota** from hatcheries and from natural nests, so filling the lack of information about the total microbial abundance and local species composition is essential for improving incubation techniques.

3.6. The Depth of the Nest

The various turtle species dig nests at different depths. Among the species highlighted in this work, the one that typically deposits its eggs deepest is leatherback (*D. coriacea*) [13] [60], followed by green (*C. mydas*) [13] [60] [81], loggerhead (*C. caretta*) [81], olive ridley (*L. olivacea*) [13], hawksbill (*E. imbricata*) [60].

Maximum nest depth seems to be determined by the size of the nesting female [11], namely by the size of the posterior legs ("paddles") used to excavate the nest chamber. At the same time, some studies, such as Marco *et al.* [82], have found that nests excavated by females of the same species, the same population or even by the individual itself differ significantly, so they consider that female length explains too small a percentage of nest depth variability to be significant, suggesting that depth is not fully explained by the size specimen. It is also uncertain whether this variability corresponds to a behavioural plasticity response to local conditions and whether there is any pattern that highlights it as a possible local adaptation to climate change.

Nest depth affects the factors that affect the conditions of the nest environment, namely **temperature** and **humidity**, conditioning the length of the incubation period, sex ratios, hatching success and the phenotype of the hatchlings.

Most research notes a **gradual decrease in sand temperature with depth**, as the deeper nests generally provide lower temperatures [60] [83]. Eggs incubated there may benefit from longer incubation periods and less female-skewing than shallower nests, and higher hatching success [82]. However, Laloë and co-authors [60] observed that this cooling effect occurred only up to about 80 cm below the sand surface, showing that **depth plays a limited role in controlling nest temperature**.

In contrast, Santos *et al.* [18] observed that the **temperature at the base of the nests sampled was higher than the sand surface temperature**, and explained that this was because the deeper sand retains solar radiation for longer. A possible explanation is that as the deeper layers are generally more humid [54] because during the heating of the beach by the sun after rain, some of the heat can be conducted downwards [57] and remain longer in the deeper layers due to the high heat capacity of water.

Nest depth also possesses the ability to stabilise temperatures. Lolavar & Wyneken [54] found that, in fact, the sand temperature in the superficial layers of the beach varied more rapidly and with a greater amplitude than in deeper layers. It has been suggested that fluctuating temperatures throughout incubation have a negative effect on embryonic development and hatchling morphology (e.g., [11]), and therefore, the depth at which eggs incubate will play a conditioning role in these two parameters.

In the **prolonged absence of rainfall**, beaches typically have a surface layer of dry sand, which allows some of the **moisture** from the layers below to be conserved [84]. However, if the nest is so shallow that it encompasses only or much of these almost entirely dry surface layers, the clutch may suffer dehydration and if the predicted reduction in rainfall combines with rising global temperatures and both parameters cause the dry sand layer to become thicker many nests may be compromised and suffer dehydration (even the least shallow ones). In addition, **drys and makes it difficult for hatchlings to rise**, and very high temperatures make them less active and probably more uncoordinated [85], so in drought conditions, if hatchlings have to travel a greater distance to the surface, the emergence rate may reduce substantially.

Simultaneously, an **increase in the frequency of extreme precipitation events is predicted** [52]. Under these circumstances, the surface layer does not have time to dry out and consequently the sand at depth becomes saturated, rainwater runs down the sand column and directly supplies the groundwater tables [9]. Rivas *et al.* [9] found that in this situation, the increased humidity-induced general mortality of eggs, especially the deepest ones, due to the rising groundwater level that flooded the nests from below. In addition, saltwater intrusion may cause nests to be inundated with more saline water, so eggs deposited deeper down may be more impacted by the detrimental effects of salinity [62].

Overall, the **advantages of depth** seem to outweigh the disadvantages and therefore some studies indicate nest **depth as the evolutionary mechanism with the greatest ability to promote the survival of sea turtle populations** [86] in a framework of global temperature increase.

3.7. Sea Surface Temperature (SST)

Air temperature and SST are strongly related. SST follows the pattern of air temperature variation, but with a **smaller range of variation** and with a **time lag** [87], given the superior heat capacity of the oceans compared to the atmosphere [4].

Most studies on the influence of temperature on sea turtles focus on terrestrial impacts [88], and less is known about the influences of elevated seawater temperatures. Knowledge of the mechanisms by which environmental factors affect physiological processes and life history characteristics of sea turtles is therefore limited, especially in marine environments, making it difficult to detect their effects on nesting parameters (but see [17]). Nevertheless, studies **so far** agree that the **effect of increased SST** on sea turtle nesting **seems to be quite complex** [89] [90], although its contribution is not as important as nest site conditions [89].

Increased SST seems to affect nesting phenology, mainly by acting as a **potential migration cue** [90], or by **altering the productivity of feeding areas** [91]. By impacting the **primary and secondary production of feeding areas**, the temperature and ocean acidification in the survival of seagrass meadows and coral reefs and the availability of prey harboured by these delicate ecosystems [89], may indirectly affect turtle nesting and reproductive output [92] [93]. Recently, changes in the abundance of benthic organisms, which constitute part of the diet of some sea turtle species, have also been detected [94].

Based on the Dynamic Energy Budget **(DEB)** model, for females to nest in a given year **they need to reach a level of body condition** that allows them to have sufficient reserves for reproductive migration [91]. **Lower food availability** essentially entails two responses: 1) A slower accumulation of energy for breeding, resulting in longer remigration intervals, interfering with reproduction rates [91] [95]; 2) A possible anticipation of the nesting time even with less available energy (to avoid too long remigration intervals), but with decreased number of clutches and fewer/clutch [91].

SST also appears to play a role in the onset of a season's nesting season [96]. Increased SST at the breeding site has already been reported to drive an early start of the nesting season [47] and change its length in some populations [97]. However, the effect of **SST on the timing of the nesting season** has been most associated with feeding areas; most studies report an early onset of the nesting season for some populations under warmer SSTs in these areas [89], but other studies have detected the opposite effect [90]. Thus, understanding the correlation between the effects of SST, on the parameters that condition phenology (not least because many of them are unclear) becomes complex.

Stubbs *et al.* [91] proposed that **increased SST in feeding areas** may also have a positive effect on sea turtle physiology by allowing energy to be assimilated and allocated faster for reproduction. However, Marn *et al.* [17] predict that this beneficial effect of SST could only occur if there is sufficient food available for the sea turtles in the foraging areas.

As for the hatchlings, several studies have laboratory tested the **swimming performance** of hatchlings exposed to **warm water temperatures** and it is agreed that this is beneficial [49], probably due to increased muscular metabolism and heart rate [98]; however, further studies are needed to confirm this. Increased nest temperature, on the other hand, negatively affects the hatchlings' swimming ability and its negative effect on swimming **seems to outweigh the positive effect** of increased water temperature, with implications for the recruitment rate of these hatchlings to the marine phase, with a decrease in it [49].

If temperatures (from SST) exceed the upper limit of the individual's thermal tolerance range, the individual may **suffer hyperthermia**. While there is substantial information on the physiological impacts of hypothermia on sea turtles (e.g., [99]), the same is not true for hyperthermia, which is a condition that some species (e.g. *E. imbricata*) may experience, for example, in the Persian Gulf [100].

Due to the physiological need of juveniles to remain in suitable water temperatures, SST drives habitat selection by juveniles and their ability to perform the full seasonal migration cycle and satisfy their food needs [101]. Thus, the two main factors that condition hatchlings' dispersal: ocean variability and the early swimming behaviour of hatchlings [99] can be influenced by SST [101], impacting key processes that influence population dynamics [102].

In addition, SST can also affect females after nesting. Ectothermia implies that these animals largely regulate body temperature **through behavioural responses**, notably by an earlier onset of returning migration or changing migration routes returning to feeding sites to experience more suitable SSTs [103].

Fuentes and co-authors [64] further suggest that increased SST may alter the sediments that are transported to nesting beaches, especially those of carbonate nature, for their contribution to coral reef degradation. Thus, the temperature of the marine environment is also predicted to play an important role in the development, phenotype, performance, dispersal ability and viability of offspring [102]. However, empirically studying the mechanisms by which SST independently affects biological processes in long-lived and globally distributed animals such as sea turtles is complicated [17], so the consequences of increasing SST for sea turtle fitness are still poorly understood.

3.8. Nest Location on the Beach

The characteristics of the nesting beach, such as its orientation, its width and length, its inclination (slope), the existence of a primary cordon with vegetation and the type of vegetation, the properties of the sediments which compose it, among other parameters, condition the nesting environment. Therefore, the selection of a place to dig and lay eggs, among a wide variety of microhabitats, will condition differently the survival and phenotype of the hatchlings.

The selection of beach sites that, in principle, favour more nest viability is an important contribution of the nesting female [41] [104]. Several studies, such as Santos *et al.* [18], suggest that sea turtles **use a combination of cues to find suitable nesting sites**, appearing to detect and select areas of higher elevation; however, it is unclear how, or whether in fact, females seek out these features. Nest elevation relative to sea level provides a variation in abiotic factors. Even if deposited in higher areas, clutches may still be partially subject to episodes of flooding, especially during high tides [41]. **Steeper beaches** can allow protecting nests from high tides and storms [105]. The inverse correlation between slope and crawl distance suggests that nesting females seek a balance between finding a safe elevation and the energy cost of crawling there, *i.e.* they do not crawl further than necessary [105].

Patrício *et al.* [41] concluded that the fine philopatry behaviour, relative to a beach/location, is due to the specific microhabitat conditions **within the beach** to establish the nest, and not the specific location itself. This would imply that to the female the microhabitat matters, on whatever beach it is.

The literature exhibits a debate on which nesting habitat characteristics lead to the selection of a certain beach site for nesting, whether females search for microhabitat thresholds (during crawling) and also what are the consequences of this selection for reproductive success [18].

It is essential to be able to identify the type of site that females seek for nesting and the characteristics that maximise incubation success in order to interpret the patterns that have been proposed and to judge if the impacts of current climate change are in fact leading species/populations to adapt their choices. And if so, how the protection of these habitats can be improved.

Within the beach, three zones with distinct characteristics are commonly considered, where sea turtles can nest: forest, border area and open area [41]. The distance to the sea essentially conditions the temperature, salinity, humidity and oxygen content of the substrate and, therefore, of the nest.

Nests closer to the sea tend to be wetter and also more prone to flooding. Embryo mortality associated with **seawater flooding** is mainly related to the increase in humidity [62] to levels above the limits tolerated by the eggs and the increase in the salt content of the sand, as even small amounts of salt in the environment outside the eggs can have a strong negative effect on embryo development by triggering an osmotic imbalance that leads to water loss by the eggs [28]. Thus, these two parameters have an overall negative effect on hatching success [62]. Nevertheless, many studies agree that **embryos have a certain tolerance to immersion** and can survive for a substantial period in saltwater, although hatching rates are significantly lower in nests subjected to these conditions [106]. However, it is predicted that more and more nests will be in this situation, mainly due to **sea-level rise (SLR)**. Over the current century, SLR will redefine the coastline and the resulting coastal erosion [107] will reduce the habitat available for sea turtles to nest, forcing them to nest closer to the water [106]. But even before habitat loss becomes permanent, SLR will unbalance terrestrial cycles by increasing the risk and changing coastal flooding regimes, particularly during storms (currently rare extreme events) that will become more common [104], and/or by inundating nests by saltwater intrusion [62].

Sea-level rise (SLR) is happening rapidly on coasts around the world, so identifying priority areas for conservation and creating trade-offs between conservation and coastal development must be established at an equally rapid pace [108]. Nest placement further inshore, avoids the disadvantages of saltwater inundation. However, it increases the likelihood of desiccation, disorientation of the hatchlings on their way to the sea and predation on both them and the females during nesting [109].

With distance from the sea, **the averages and temperature** tends to increase. It is in the intermediate zone where maximum temperatures often occur [21] and where greater female bias in nesting is consequently expected. Fuentes *et al.* [2] further observed that the incubation environment in this beach zone may be **even warmer depending on beach orientation**.

Finally, dune vegetation, or even forest found after the beach, may have advantages for incubation. It prevents nest inundation due to sea-level rise (SLR) as it is generally located in higher areas, provides a potential refuge for nesting females and provides cooler incubation temperatures by shading the nests [110]. However, **root infiltration into the nests often impairs** the rise of the hatchlings to the beach surface [41].

Different species of sea turtles have nesting preferences, within the beach and tend to nest in specific areas. For example, *E. imbricata* tend to nest at the back of the beach, close to vegetation [111]. *C. caretta* nest in the mid-zone of the beach [111], regardless of the width of the beach [5]. *D. coriacea* nest more frequently near the **HTL (high tide line)** when compared to any other species [53]. This typical nest location in certain areas of the beach explains much of the acknowledged low hatching success of *D. coriacea* relative to other sea turtles, as the close proximity to the sea results in a higher probability of nest inundation, especially with the current SLR [106].

It is also predicted that *C. caretta* will have a similar problem in the future, because as they tend to nest in the middle of the beach, increased coastal erosion, as a result of SLR [5], will cause nests to be established closer and closer to the water.

As for the nests of *C. mydas*, if on the one hand by being commonly deposited on the dune cordon, close to vegetation, they can benefit from shade, they are also often subject to the intrusion of plant roots that entangle the hatchlings, reducing emergence success [41]. Zavaleta-Lizárraga and Morales-Mávil [112] suggest that green turtles consider the existence of vegetation as a signal for the existence of sites with a thin and moist substrate, which they seem to prefer. Additionally, green sea turtles generally prefer beaches without obstacles such as rocks, steep slopes, or coastal development, *i.e.*, where access from the sea and movement of females on the beach is easy [18].

Unlike the other sea turtle species, the nest-site selection for *Lepidochelys olivacea* is scarce [113]. The populations studied by Ávila-Aguilar [113] showed a strong preference for nesting as far away from the HTL as possible, regardless of beach width, suggesting that protecting the clutch from tidal inundation is the priority, regarding the longer journey to the ocean for both adult females and hatchlings.

3.9. Nesting Phenology

The **phenological changes that have been detected at various nesting sites** are seen as **one of the potential strategies likely to mitigate the effects of climate change**. They appear to offer the opportunity to use an **optimal thermal window** during a critical period that impacts ultimate reproductive success [3]. However, these changes may entail problems. It is estimated that mismatches can occur **between** predicted changes in other climatic parameters (such as precipitation) [3].

In the **long-term**, these potential desynchronizations could convert a given phenological change into a maladaptive response that may even jeopardize the **fitness and viability of populations**. Nevertheless, altering the timing of nesting has been discussed as an effective strategy to deal with short-term climate warming and as a way to allow successful nesting and incubation in some breeding sites and for some populations.

Some species **have more fixed nesting patterns** than others and may be more subject to environmental unpredictability than more flexible species [114]. For example, while *C. caretta* is likely to alter the timing of nesting in the face of warming environments at the nesting site, the nesting season of *C. mydas* is presumed to remain relatively fixed, given its lack of flexibility regarding nesting timing [114]. However, more recent studies such as Anastácio *et al.* [115] have detected a dislocation of peak nesting activity in the Vamizi population of green sea turtles, suggesting some behavioural plasticity.

Laloë, Esteban, Berkel and Hays [60] found that nests of *D. coriacea* nesting in St. Eustatius (Caribbean) had, on average, higher feminized sex ratios than nests of *E. imbricata*, due to the former nest during the warmest months of the year, while the latter nest for 10 months of the year, therefore also covering colder periods. In species whose nesting season encompasses both hot and cold periods of the year, there may be sufficient fluctuation in temperature to cause sex ratios to vary substantially within a single nesting season. For example, in Kochi (Japan), where the temperature increases throughout the *C. caretta* nesting season, Kobayashi *et al.* [27] found that nests established early in that period produced significantly more males, due to lower incubation temperatures, compared to nests established late in the season, whose high incubation temperatures led preferentially to the production of females which confirms the previous reasoning. The cooler times of the nesting season provided by temperate climates are seen as temporal **microrefugia** for male production. **Microrefugia** are understood as the "existence of conditions that would be more suitable for population persistence under global warming scenarios, both in space (*i.e.*, more suitable microhabitat), and in time (*i.e.*, periods of the year with lower incubation temperatures)" [110]. It may happen that females alter the start date of the nesting season in an attempt to coincide with these temporal windows in which the temperature is more favourable, but the length of the season remains stable [96]; the return of females to feeding sites may be anticipated or delayed in parallel [103]. Therefore these phenological changes do not always mean advantages, as they can expose populations to higher SST's during migrations (such as those of Mediterranean *C. caretta* [103]) or potentiate mortality of post-hatching hatchlings during their oceanic dispersal leading them to experience hypothermia [99]. Thus, as has been discussed, for these highly migratory animals whose certain life cycle events seem to be related to signals detected at relatively distant locations (e.g., nesting beaches, route migrations and foraging habitats), we can expect that changes in the conditions at these locations may influence their phenological responses.

In temperate locations, the anticipation of the nesting season may allow similar incubation climatic conditions to those currently found during the nesting season, as it is likely that the months of the year that **currently record temperatures** too low for egg development will now provide suitable thermal conditions due to climate warming [56]. On the other hand, climatic conditions are predicted to **become increasingly dry and hotter**, and even if nesting starts earlier. Therefore, these phenological adjustments may not be sufficient to sustain current populations in the long term [47].

In **tropical locations**, Tomillo *et al.* [56] predict that climate warming will cause atmospheric temperatures to be several degrees above current seasonal averages during the coldest months. In these regions, a shortening of the nesting season is likely to occur, as the hot and dry weather conditions predicted for the months before and after the current nesting season may act as thermal barriers.

On the **nesting beach** itself, even if changing the timing of the start of the season allows populations to select cooler months, this change may not be adequate to follow the changing patterns of other climatic factors, such as precipitation [3]. Thus, these responses may only partially offset the impacts of climate change on nesting and incubation. It is anticipated that in specific locations it may be **possible to offset the impact of climate change on incubation** by adjusting the nesting season to occupy times of the year more conducive to successful incubation. However, this ability may not be representative of the entire population and is likely to be **effective only in the short-term** due to the accelerated rate at which climatic conditions are occurring, translating into a climate debt, *i.e.* a time gap between the phenological changes required and those expected or observed [25].

What about feeding/development sites? As explored in the topic 3.7, studies suggest that in addition to air (and sand) temperature, SST in feeding areas play an important role in the interval between nesting seasons and the timing of the season itself, essentially by conditioning food availability, or as a cue to initiate reproductive migration. Thus, sea turtles may need to respond to two sets of cues, in the feeding habitat and the breeding habitat [90]. However, the fact that the parameters driving reproductive migration and nesting may interact and mask (or influence) the effect of each other makes them remain uncertain. The **complexity of the cues** and **variability in the response** of populations and species makes it hard to understand and predict how changes in the parameters that provide these signals might impact the reproductive success of sea turtles [90].

Given the complexity of analysing these phenological responses, Monsinjon *et al.* [25] suggest that, in the future, attempts should be made to combine changes driven by resource alteration and climate change in time and space to predict the adaptive potential of species and populations to climate change.

3.10. Geographic Distribution of Nesting Habitats

The persistence of sea turtle species and populations depends on the **ability to adapt to new conditions locally** (phenotypic adaptation), or to **adjust to new environments** (behavioural/phenological plasticity) [116].

The **first hypothesis** could be the most predictable given the recognised natal philopatry of sea turtles and their long maturation and life span. Indeed, on some specific beaches, there **seems to be evidence of local adaptations** [66], but this aspect is still under debate. On one hand, philopatric behaviour can lead to a **reduction of gene flow** between populations and genetic diversity; and thus, the **adaptive potential erosion** in populations according to some authors

[117]. On the other hand, philopatry can be seen as able to conserve adaptive potential by promoting the **retention of locally adapted genetic polymorphism**, while an **asymmetric flow** is provided by transient males, which can maintain connectivity with other populations [117].

In the absence of genetic adaptation, populations may need to respond rapidly to climate change impacts on their breeding habitats through behavioural plasticity [22]—the **second hypothesis**. In the longer term, it is likely to be individual plasticity that may confer population adaptive potential [22], through adjustment of nest depth, nest site selection, altered nesting phenology and redistribution of nesting area. **Changes in the geographical distribution** of **nesting habitats** can occur despite the acknowledged philopatry of females because when selecting a nesting area during first breeding, the female does show strong fidelity not specifically to that beach, but to the area in which the beach is inserted [4]. Through some environmental cues, that remain uncertain, in some studies (e.g., [118]) it's hypothesised that females can predict whether a nesting beach is suitable for offspring production [118]. Females may nest on different beaches during a nesting season and between seasons, so they are expected to change nesting habitat if it is unsuitable, especially for those who are choosing their first beach [119]. On the other hand, the accuracy of natal homing probably varies considerably between populations and species [120], so the ability to execute these changes is variable.

The results of the study by Stokes *et al.* [121] suggest that *C. mydas* neophytes have been showing a **decrease in nest-site fidelity**, and that these exploratory behaviours can promote resilience to breeding site loss [121].

The speed and magnitude of these changes will depend not only on the degree of nest site fidelity but also on the geographical characteristics of the original beach. For example, nesting at higher latitudes where incubation conditions must be cooler is unlikely for sea turtles nesting in the Cape Verde Archipelago, as the nearest island under such conditions is hundreds of kilometres away [122]. Whereas if a beach disappeared along a continuous coastline, females do not, in theory, need to move much to find alternative nesting habitats [123]. Thus, the persistence of populations in a habitat whose nesting site has either disappeared or is no longer suitable will depend on the **existence of other pre-existing beaches that have suitable conditions** [123].

Newly established beaches may host new populations; however, the existence of beaches with such incubation and nesting characteristics and which can compensate for the costs of reproductive migration could be not so common.

To predict whether populations will successfully establish themselves in new territories it is essential to understand if the **spatial changes** will be accompanied by **increased exposure to other threats** [124]. For example, in Australia a movement of loggerhead nesting populations southwards in response to increasing temperatures in the north was detected; however, these beaches were at much higher risk of SLR, so this adaptation likely led females to nest in suboptimal conditions [123].

The **lack of consensus on the environmental cues** used by females **in choosing nesting sites** hampers the prediction of changes in the distribution of nesting areas [125] in response to climate change and coastal development, therefore, makes it difficult to recognize and model the best areas to focus mitigation and conservation efforts.

Currently, the distribution of sea turtle nesting areas covers mostly tropical or subtropical climates and, with a lesser expression, temperate regions, with the range of nesting habitats varying between species [118].

It is unclear whether the pace of climate change intensification, namely temperature increase, will allow **phenotypic adaptation**; if they are not able to keep up with the climate change trends, local anthropogenic mitigation may become the only way to preserve populations at risk [116]. Although indispensable, might not be enough to "compensate for the lack of global action in reversing trends" [58]. It should be noted that efforts need to be focused on areas with the greatest future potential, but also on those that currently support nesting because responses to climate change are not fixed or uniform, and therefore some populations may not choose to expand their geographic distribution.

The reasons for sea turtles expanding their geographic range appear to be primarily **temperature increases on nesting beaches** and **loss of nesting territory** due to **SLR, extreme weather events, erosion** and **human development**. Nests established by populations nesting in **tropical environments** are naturally located near the upper margin of the embryo's thermal tolerance range, so global temperature increases are predicted to cause a severe decline in hatching success [126] and consequently jeopardise the stability of these populations. In **temperate regions,** on the other hand, hatching success is predicted not to change substantially, or to initially increase with moderate warming, followed by a decline under continued long-term warming [126]. The **milder climate** allows a greater distance to the thermal margins that delimit the decline in hatching success, so species with populations that nest in temperate regions may show greater resilience than those whose populations only nest in regions with tropical climates [56]. However, the variation in environmental conditions at the local level implies that different nesting sites also respond in different ways to climate change [56], so there is also a need to monitor their change and assess their effects on reproductive output and the response of populations at small scales and across a wide variety of distant locations.

4. Conclusions

Efforts have been made worldwide to protect sea turtle species from extinction driven by human-induced constraints (which include climate change as well as direct threats e.g. poaching).

Most of the measures taken involve protecting nesting habitats, preventing the hunting of nesting females and their eggs, and protecting nests, from relocating them to safer locations on the beach to constructing artificial nurseries that seek to replicate optimal incubation conditions.

However, for these measures to be effective enough to mitigate the effects of changes to ensure the survival of the species, it is still necessary to overcome several challenges, including: 1) Knowing the influence of abiotic parameters (mainly temperature, humidity and salinity) and biotic (characteristics of the mother and the offspring itself, microorganisms); 2) Which sites present the best characteristics, in time and space, taking into account climate change, *i.e.* which beaches and which characteristics of these beaches should be conserved as a priority; 3) Discover how to create an artificially optimal environment; 4) Increase our understanding of the marine phase of sea turtles' life, in addition to its influence on the terrestrial reproductive phase.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

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