Ana Laura Ferreira Lopes

"Effects of *in situ* Incubation Environment on Hatchling Morphology and Fitness in the Northern Gulf of Mexico on Loggerhead Sea Turtles (*Caretta caretta*)"

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Resumo

A tartaruga-comum (*Caretta caretta*), pertencente à família *Cheloniidae*, é uma espécie de tartaruga marinha com uma distribuição global ampla, predominando em regiões subtropicais e temperadas dos oceanos Atlântico, Índico e Pacífico. O seu ciclo de vida é composto por quatro fases: recém-nascido, juvenil, subadulto e adulto, com diferenças visíveis na coloração e tamanho, atingindo a maturidade sexual entre 22 e 50 anos, reproduzindo-se a cada dois a três anos. A tartaruga-comum alimenta-se de uma variedade de espécies, incluindo decápodes, bivalves, gastrópodes, alforrecas, esponjas e, ocasionalmente, algas. Habitando ambientes distintos ao longo da vida, as tartarugas-comum iniciam sua vida em praias arenosas, migram para o oceano aberto e, eventualmente, retornam a habitats costeiros para a reprodução. Apesar de serem essenciais para os ecossistemas, as tartarugas-comum enfrentam várias ameaças naturais e antropogénicas. Na fase de desova, ovos e recém-nascidos são alvo de predadores como guaxinins, raposas e aves marinhas, enquanto no ambiente marinho, juvenis e adultos enfrentam predadores como tubarões. Doenças como a fibropapilomatose também ameaçam a sua sobrevivência. As alterações climáticas aumentam a temperatura da areia, podendo desequilibrar a proporção de sexos dos recém-nascidos e piorar as condições das praias de desova. A ação humana intensifica essas ameaças, com o desenvolvimento costeiro, poluição luminosa e resíduos plásticos, prejudicando o ciclo de vida das tartarugas. A captura acidental em redes de pesca e as colisões com embarcações representam graves riscos, levando à morte ou ferimentos severos de muitos indivíduos. Devido a essas ameaças, a tartaruga-comum, inicialmente classificada como ameaçada, está atualmente listada como vulnerável na Lista Vermelha da IUCN.

As condições ideais para a nidificação envolvem uma combinação de características de praia e fatores ambientais adequados. Dois fatores que afetam vários aspetos do desenvolvimento embrionário, incluindo o crescimento dos embriões, sexo e sucesso de eclosão, são a temperatura e a humidade do ninho. Temperaturas baixas (26–28 °C) produzem principalmente machos e abrandam o metabolismo, resultando em recém-nascidos maiores; a temperaturas intermédias (28–30 °C), ambos os sexos são produzidos em proporções aproximadamente iguais; e a temperaturas altas (30–34 °C) predominam as fêmeas e aceleram o metabolismo,

levando a recém-nascidos menores, desenvolvimento mais rápido e maior risco de anomalias. Com as alterações climáticas, o aumento da temperatura pode criar um desequilíbrio da proporção de sexos, eclodindo mais fêmeas. O nível de humidade atua sobre a regulação das troca gasosas e do equilíbrio hídrico. O aumento da humidade, está associado a incubações mais longas, mais machos e a humidade excessiva pode mesmo levar à hipóxia e a desenvolvimentos anómalos. A temperatura e humidade também afetam características morfológicas e a aptidão física, podendo influenciar a coordenação muscular, flutuabilidade, agilidade e resistência física dos recém-nascidos, prejudicando sua capacidade de navegar com sucesso em direção ao oceano. O tamanho, o peso e as reservas de energia, regulados por diversos fatores ambientais e genéticos, influenciam a capacidade dos indivíduos se endireitarem (quando estão de costas, com a carapaça na areia, e precisam de se virar para seguir em direção ao mar) e de locomoção (tanto em ambiente terrestre como aquático) dos recém-nascidos.

A literatura existente revela lacunas na compreensão específica de como os fatores ambientais afetam os recém-nascidos de tartarugas marinhas. Grande parte da investigação concentra-se em variáveis isoladas, sem estudar os efeitos combinados de múltiplos fatores, como temperatura, humidade, tipo de areia e níveis de oxigênio, que podem influenciar simultaneamente a aptidão física e a morfologia dos recém-nascidos. Além disso, a maioria dos estudos existentes foca-se principalmente em duas espécies, como a tartaruga-comum e a tartaruga-verde, descurando o estudo das restantes. Como cada espécie pode responder de maneira diferente às variáveis ambientais, é essencial realizar estudos mais inclusivos para entender essas respostas específicas e melhorar os esforços de conservação. Outro ponto importante é a cobertura geográfica, já que a maioria dos estudos são realizados em regiões específicas, como Queensland, na Austrália, e Flórida, nos EUA, que são zonas de nidificação muito importantes. Para compreender a influência dos fatores ambientais em diferentes contextos geográficos, é fundamental expandir a pesquisa para incluir uma maior diversidade de locais. Além disso, muitos estudos têm sido de curto prazo, limitando-se a uma única época de desova, o que dificulta a compreensão do impacto da variabilidade sazonal e das mudanças ambientais a longo prazo no desenvolvimento dos recém-nascidos.

Vários estudos investigaram os efeitos da temperatura e da humidade na aptidão física e morfologia dos recém-nascidos, predominantemente em condições laboratoriais ou por meio de perturbações dos ninhos/ovos. No entanto, compreender estes impactos em incubação natural é essencial. O presente trabalho visa preencher essa lacuna, avaliando os efeitos combinados de temperatura, humidade e morfologia na aptidão dos recém-nascidos da tartaruga-comum no seu ambiente natural. Os principais objetivos são: (1) aprofundar a compreensão de como as condições de incubação *in situ* influenciam a aptidão física e morfologia das tartarugas-comum (*Caretta caretta*) e (2) investigar o impacto das características morfológicas na sua aptidão física. Para alcançar estes objetivos, foram recolhidos dados na Ilha de St. George, Florida, Estados Unidos da América, durante a temporada de 2022. A Ilha de St. George alberga a maior agregação de tartarugas-comuns na Unidade de Recuperação do Norte do Golfo do México. Os dados recolhidos incluíram variáveis ambientais como a temperatura — temperatura média durante a incubação, e as temperaturas médias para cada terço do período de incubação — e parâmetros de inundação — intensidade da inundação, frequência de inundação e duração total da inundação — bem como aptidão física e medições morfológicas detalhadas dos recém-nascidos. As variáveis morfológicas medidas foram o peso, o comprimento e a largura da carapaça, o comprimento do plastrão, a largura da cabeça, o comprimento e a largura da cicatriz umbilical e o comprimento da barbatana. Estas variáveis foram usadas para entender como as condições ambientais e a morfologia afetam a aptidão física dos recém-nascidos de tartaruga-comum — tempo de endireitamento e velocidade de locomoção terrestre.

As hipóteses a testar foram que temperaturas mais altas de incubação e inundação periódica reduziriam a aptidão física dos recém-nascidos, enquanto características morfológicas como o peso, o comprimento da carapaça e das barbatanas teriam uma influência significativa na aptidão física. Os resultados mostraram que o peso dos recém-nascidos é proporcional ao tempo de endireitamento, com recém-nascidos mais pesados a demorarem mais tempo a endireitar-se. O comprimento da carapaça influenciou significativamente a velocidade de locomoção terrestre, sendo que carapaças mais longas resultaram em deslocações mais rápidas. Contudo, a inundação e o comprimento das barbatanas não tiveram impacto significativo na aptidão física. Apesar de a temperatura não ser estatisticamente significativa relativamente ao endireitamento, temperaturas médias mais altas foram associadas a um tempo de endireitamento mais demorado. Em termos morfológicos, temperaturas mais elevadas de

incubação resultaram em recém-nascidos menores e mais leves, em alinhamento com os resultados de estudos anteriores. A inundação não afetou a morfologia nem a aptidão física, o que poderá ser explicado pelas limitações deste estudo, como o tamanho reduzido da amostra. O presente trabalho tem reconhecidas limitações, entre as quais se destacam o tamanho da amostra — somente 80 indivíduos em quatro ninhos —, a restrita cobertura geográfica e temporal — estudo numa única temporada e localização —, e a ausência de consideração de outros fatores ambientais e genéticos. Este estudo contribui para o conhecimento existente sobre os impactos regionais da temperatura e inundação nas características morfológicas e na aptidão física, corroborando investigações anteriores quanto à influência da temperatura, mas sem encontrar efeitos significativos da inundação. Estudos futuros deverão considerar estas limitações e realizar investigações mais abrangentes, incluindo outros fatores, para aprofundar a compreensão do desenvolvimento e aptidão física dos recém-nascidos. É fundamental para o desenvolvimento de estratégias de conservação eficazes e para garantir a sobrevivência a longo prazo das populações de tartarugas marinhas que se continue a desenrolar este tipo de investigação.

Abstract

Incubation conditions significantly influence various traits in reptilian neonates, a critical consideration for species like sea turtles. This study aims to understand how these conditions, particularly nest temperature and inundation, affect the morphology and fitness of loggerhead sea turtle (*Caretta caretta*) hatchlings. Temperature has been extensively studied among these conditions, revealing its profound effects on hatchling traits such as sex determination and growth rates. However, the role of nest inundation, which can also alter developmental outcomes, remains underexplored, despite its impact on hatchling size, sex, incubation duration, and hatching success. Previous studies often used relocated or laboratory-reared nests, which do not accurately reflect natural temperature fluctuations. To address this gap, we monitored *in situ* incubation conditions on St. George Island, Florida, during the 2022 nesting season by deploying temperature and water data loggers in seven loggerhead nests, although only data from four nests were usable for analysis. Upon hatchling emergence, eight morphological traits were measured, and fitness was assessed through self-righting time and crawl speed tests. Statistical analysis revealed that hatchling mass was a significant predictor of self-righting time, with heavier hatchlings taking longer to right themselves. Additionally, faster crawl speeds were associated with longer carapaces. Although temperature was not statistically significant, higher average temperatures were associated with slower self-righting time. Incubation at higher temperatures resulted in smaller and lighter hatchlings, consistent with previous studies, while inundation did not affect the morphology or fitness of hatchlings. These findings contribute to the existing knowledge of hatchling incubation effects, offering new insights into how regional environmental conditions influence hatchling development and fitness. However, the small sample size and focus on a single nesting season limit the generalizability of these results, suggesting a need for further research.

Keywords: *Caretta caretta*, temperature, inundation, morphology, self-righting time, and crawl speed

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List of Abbreviations

AICc - Akaike's Information Criterion

BD - Body Depth

BIC - Bayesian Information Criterion

Cc - *Caretta caretta*

CITES - Convention on International Trade in Endangered Species

Cm - *Chelonia mydas*

CS - Crawl Speed

Dc - *Dermochelys coriacea*

FL - Flipper Length

FW - Flipper Width

HW - Head Width

I_D - Total Inundation Duration

I_F - Frequency of Inundation

I_S - Inundation Severity

IUCN - International Union for Conservation of Nature

LMM - Linear Mixed Models

Lo - *Lepidochelys olivacea*

LogLik - Log-Likelihood

M - Moisture

Mass - Hatchling Mass

MPAs - Marine Protected Areas

Nd - *Natator depressus*

NGMRU - Northern Gulf of Mexico Recovery Unit

R^2c - Conditional R^2

R^2m - Marginal R^2

RMU - Regional Management Unit

RT - Self-Righting Time

SCL - Straight Carapace Length

SCW - Straight Carapace Width

SGI - St. George Island

SPL - Straight Plastron Length

T - Temperature

T1 - Average Temperature for the First Third of the Incubation Period

T2 - Average Temperature for the Second Third of the Incubation Period

T3 - Average Temperature for the Third Third of the Incubation Period

TEDs - Turtle Excluder Devices

Temp - Average Temperature During Incubation

TSD - Temperature-Dependent Sex Determination

USL - Umbilical Scar Length

USW - Umbilical Scar Width

Sea turtles have been around for millions of years, witnessing the rise and fall of empires. Their struggle today reflects the environmental changes threatening their ecosystems—one that demands our immediate attention.

Chapter I

General Introduction

1. THE SPECIES - *CARETTA CARETTA* (LOGGERHEAD SEA TURTLE)

1.1 Species Overview

The loggerhead turtle, *Caretta caretta* (Linnaeus, 1758), was named for its large, heavy head, and robust skull (Dodd, 1988), 'loggerhead' originally comes from the English word "log", meaning a heavy block of wood, which was used in reference to the turtle's big head. Loggerheads belong to the *Cheloniidae* family (Spotila, 2004), they are one of seven marine turtle species globally and one of five found in the Northern Gulf of Mexico (NOOA, 2022). The *Cheloniidae* family is believed to have emerged around 25 million years ago (Cadena et al., 2018; Thomson et al., 2021), and loggerheads around 10 million years ago (Fitzgerald & Kool, 2014). *Cheloniidae* includes other well-known species such as the green, olive ridley, hawksbill, flatback, and Kemp's ridley sea turtles (Bowen, Nelson, et al., 1993; Spotila, 2004). Despite its morphological resemblance to the green turtle, the loggerhead is genetically closer to the Kemp's ridley, olive ridley, and hawksbill sea turtle (Bowen, Nelson, et al., 1993; Spotila, 2004).

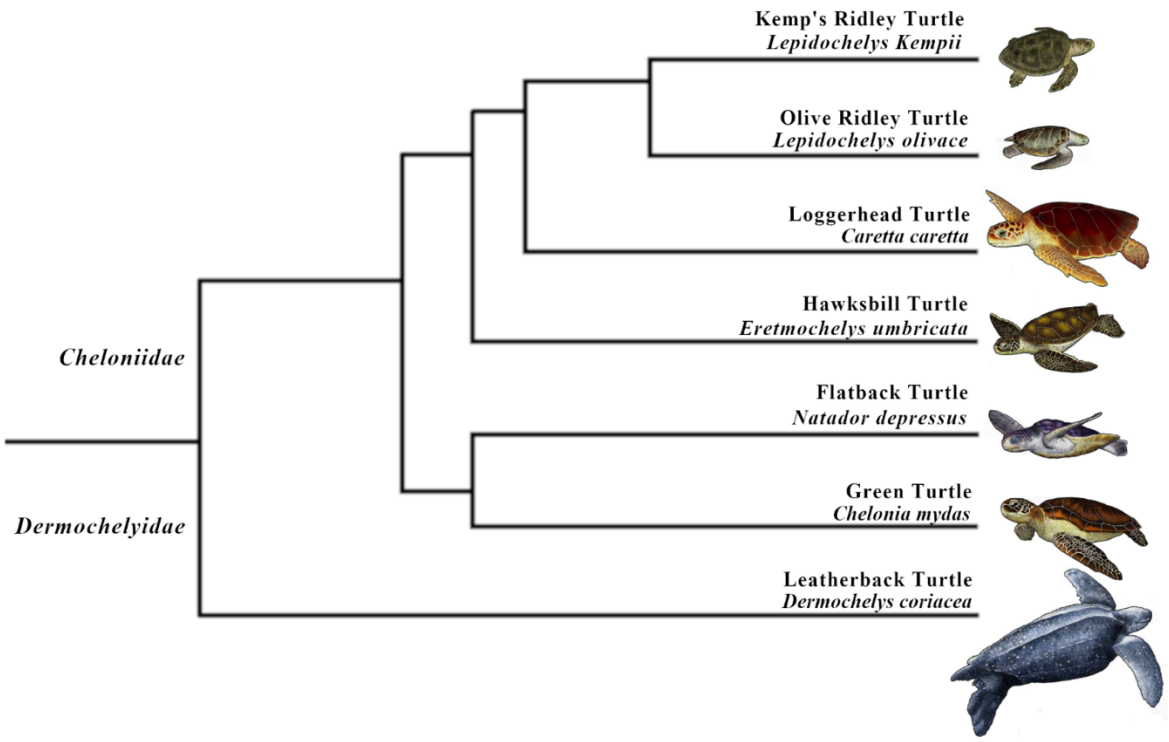

Figure 1.1. Sea turtle phylogeny (Galatoulas, 2021).

Loggerheads are globally distributed, primarily found in subtropical to temperate regions of the Mediterranean Sea, Atlantic, Indian, and Pacific Oceans (Bowen et al., 1995; Boyle et al., 2009; Casale et al., 2013; Lohe & Possardt, 2021; Monzón-Argüello et al., 2009). Its range extends from as far north as Canada, the United Kingdom, and Japan or as far south as Argentina, South Africa, New Zealand, and Australia (Baldwin et al., 2003; Margaritoulis et al., 2003; Spotila, 2004). Additionally, significant nesting aggregations occur in Peninsular Florida, USA; Masirah Island, Oman; Boa Vista Island, Cape Verde (Marco et al., 2011; Mrosovsky & Provancha, 1989; Rees et al., 2010).

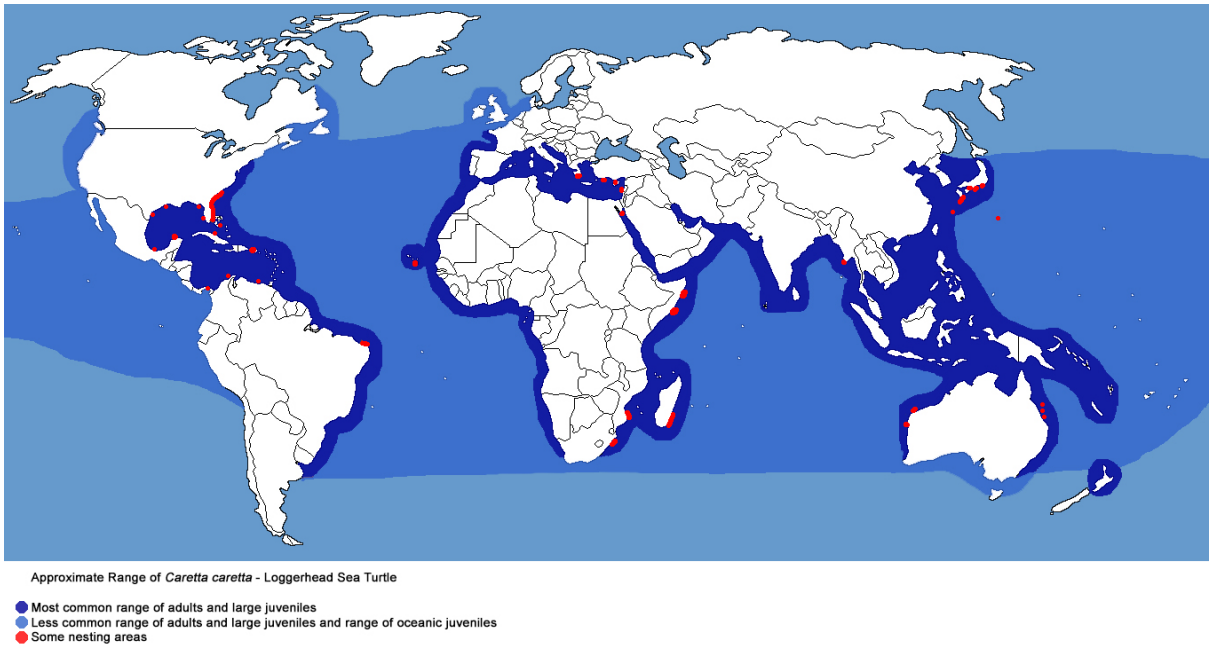

Figure 1.2. Approximate distribution map of the loggerhead turtle's dispersal range worldwide (Nafis, 2024).

Adult loggerheads typically range from 80 to 109 cm in length and 61 to 99 cm in width (Marn et al., 2015), and weigh around 110 kg on average (Marn et al., 2019). Their life cycle includes four stages: hatchling, juvenile, subadult, and adult (Dodd, 1988). Morphologically, these stages exhibit differences in coloration and size. Hatchlings are darker, measuring about 4.5 cm and weighing approximately 20 g (Mcgehee, 1990). Juveniles have lighter coloration and grow to about 60 cm in length (Marn et al., 2015). Adults have a large head, powerful jaws, an orange to brown hard carapace, a pale-yellow plastron, and pale-yellow skin adorned with brown spot-like patterns (Dodd, 1988; Pritchard & Mortimer, 1999; Spotila, 2004).

Loggerheads are omnivorous, utilizing their strong jaws to feed on a variety of hard-shelled animals such as decapods, bivalves, and gastropods (Plotkin et al., 1993). Their diet is the most diverse among sea turtles (Tomas et al., 2001) and also includes softer organisms like jellyfish, sponges, and occasionally seaweed (Palmer et al., 2021). Their feeding habits vary across life stages.

1.2. Life Cycle

The life cycle of the loggerhead sea turtle (*Caretta caretta*) comprises four distinct stages: egg, hatchling, juvenile, subadult, and adult (Dodd, 1988). Loggerhead sea turtles are estimated to reach their sexual maturity from 22 to 50 years of age, with their post-maturation longevity ranging from 4 to 46 more years, with an average of 19 years, differing significantly between individuals (Avens et al., 2015). Mating occurs every two to three years (Broderick et al., 2002; Lasala et al., 2018), usually from March to early June (Manire et al., 2008), and they can be mated to multiple male partners (Bollmer et al., 1999; Moore & Ball, 2002). The nesting season typically spans from April to September (Margaritoulis, 2005; Martins, Patrício, et al., 2022; Pike, 2008), with females laying on average 3 to 5.4 nests per season (Broderick et al., 2002; Lasala et al., 2018). The timing of mating and nesting seasons is not fixed and can vary between different populations (Hatase et al., 2008; Tiwari & Bjorndal, 2000).

Loggerhead turtles are highly migratory but return to their birthplace to lay eggs on sandy beaches (Avens et al., 2003; Avens & Lohmann, 2003; Tucker, 2010). Each clutch contains approximately 100 to 120 eggs (Dodd, 1988; Mcgehee, 1990; Miller et al., 2003). After an incubation period of about 45 to 70 days, influenced by ambient temperature, the eggs hatch (Dodd, 1988; Miller et al., 2003). Environmental temperature is crucial for successful incubation, with eggs requiring a narrow temperature range of 25 to 35 °C to hatch (Blanck & Sawyer, 1981; Fisher et al., 2014; Howard et al., 2014a). Within this range, the specific temperature and chemical conditions of the sand can affect the growth, morphology, and gender of the embryos (Carthy, 1996; Yntema & Mrosovsky, 1980).

A loggerhead turtle inhabits three distinct habitats throughout its life. Born in a sandy terrestrial environment, hatchlings that safely reach the sea begin a long oceanic migration using major currents (Cardona et al., 2018; Luschi et al., 2003). Upon reaching the ocean, the hatchlings enter a pelagic phase, during which they inhabit the open ocean and drift with the currents (Bjorndal et al., 2000). They travel to the oceanic zone where they spend their juvenile years (Bolten, 2003). As they grow, in the subadult stage loggerheads transition from the pelagic phase to more benthic, coastal habitats where they accumulate energy reserves necessary for

maturation and eventual reproduction (Hatase et al., 2008). After several years, upon reaching sexual maturity, the adult sea turtles return to the nearshore ecosystems, until mating in their natal rookery to nest (Avens et al., 2003; Avens & Lohmann, 2003; Tucker, 2010), which restarts the cycle of a sea turtle journey.

1.3. Threats to Loggerheads

Loggerhead sea turtles (*Caretta caretta*) are a species that face a myriad of threats throughout their life cycle. These threats can be broadly categorized into natural and human-induced.

Natural Threats

Loggerhead sea turtles encounter several natural threats, particularly during their early life stages on nesting beaches. Predation is a significant risk, with eggs and hatchlings being particularly vulnerable (Stewart & Wyneken, 2004). Common predators include raccoons, foxes, lizards, ghost crabs, and seabirds (Butler et al., 2020; Lei & Booth, 2017; Marco et al., 2015; Yerli et al., 1997). These predators can decimate entire nests, significantly reducing hatchling survival rates (Martins et al., 2021). In the marine environment, juvenile and adult loggerheads are preyed upon by sharks and large predatory fish (Bornatowski et al., 2012; Heithaus et al., 2005, 2008). The predation risk decreases as turtles grow larger, but it remains a constant threat throughout their lives (Stewart & Wyneken, 2004).

Diseases also pose substantial risks to loggerhead populations (George, 2017). Fibropapillomatosis, caused by a herpesvirus, is one such disease that can have severe impacts (Lackovich et al., 1999). This condition leads to the development of tumors on the skin, eyes, and internal organs, impairing a turtle's ability to swim, feed, and see, which ultimately affects their survival and reproductive success (Lackovich et al., 1999; Lawrance et al., 2018; Page-Karjian et al., 2015).

Climate change is an overarching threat that exacerbates many existing issues (Fuentes et al., 2011; Hawkes et al., 2009). Rising temperatures affect sand temperatures on nesting beaches, which influences the sex ratios of hatchlings due to temperature-dependent sex determination (Morreale et al., 1982; Standora & Spotila, 1985). Warmer sands generally produce more females, potentially leading to skewed sex ratios that can affect future breeding populations, or failing incubation altogether (Fuentes et al., 2010; Hawkes et al., 2009; Telemeco et al., 2013). Additionally, climate change is predicted to increase the frequency and intensity of extreme weather events (Montero et al., 2018), further impacting nesting sites and turtle populations.

Extreme weather events, such as hurricanes, heatwaves, and tropical storms, can have devastating effects on loggerhead populations (Hays et al., 2021; Laloë et al., 2021; Rivas et al., 2018). These events can erode nesting beaches, wash away nests, and directly cause the death of hatchlings (García-Carcel and López-Jurado, 2005). Moreover, such weather phenomena can alter the physical characteristics of nesting sites, making them less suitable for future nesting (Fuentes et al., 2011; García-Carcel & López-Jurado, 2005).

Human-Induced Threats

Human activities have dramatically intensified the threats faced by loggerhead sea turtles. Coastal development is one of the most significant human-induced threats, leading to the loss of nesting habitats (Lutcavage et al., 2017; Mazaris et al., 2009). Construction of buildings, seawalls, and other infrastructure can destroy or degrade nesting beaches, making them unsuitable for egg deposition (Rizkalla & Savage, 2011; Salmon et al., 1995). Light pollution from coastal development further exacerbates the situation (Longcore & Rich, 2004; Salmon & Witherington, 1995; Vandersteen et al., 2020). Hatchlings rely on natural light cues to find their way to the ocean, and artificial lighting can disorient them, causing them to head inland where they are more vulnerable to predation and dehydration (McFarlane, 1963; Silva et al., 2017).

Marine pollution presents another severe threat to loggerheads (Bugoni et al., 2001; Carr, 1987). Plastic debris and chemical contaminants in the ocean can lead to ingestion and entanglement (Moon et al., 2023; Novillo et al., 2017). Loggerheads often mistake plastic items for food, leading to ingestion that can cause blockages, malnutrition, and death (Pham et al., 2017; Ryan et al., 2016). Chemical pollutants, such as heavy metals and persistent organic pollutants, can accumulate in the tissues of sea turtles, causing toxic effects and impacting their health and reproductive success (Novillo et al., 2017).

Fisheries bycatch is one of the most significant anthropogenic threats to loggerhead sea turtles. Turtles are frequently accidentally captured in various types of fishing gear, including trawls, longlines, and gillnets (Casale et al., 2007; Martins, Tiwari, et al., 2022; Wallace, Lewison, et al., 2010). Bycatch can lead to injuries or death from drowning, as turtles become trapped and unable to surface for air (Tomás et al., 2008). As well as vessel collisions, turtles can be hurt by impact, causing substantial damage such as severe cuts and amputations (Fuentes et al., 2021; Hazel & Gyuris, 2006).

1.4. Ecological Role and Conservation

Sea turtles are essential for marine ecosystems, serving multiple ecological roles that contribute to the health, nutrient cycling, and stability of their ecosystems (Wyneken et al., 2013). As omnivorous predators, they help regulate the populations of their prey, contributing to the health of seagrass beds and coral reefs, maintaining the balance of marine food webs (Bjorndal, 2017). Their nesting activities also facilitate nutrient cycling, as unhatched eggs and hatchlings remains provide essential nutrients for dune vegetation, enriching the nutrient-poor sandy soils of nesting beaches (Le Gouvello et al., 2017).

The conservation of loggerheads is important not only for their survival but also for the overall health of marine environments. Initially, loggerheads were classified as a threatened species in 1978 under the Endangered Species Act (U.S. Fish & Wildlife Service) (Stromberg, 1979). Currently, they are listed as vulnerable by the International Union for Conservation of Nature

(IUCN) Red List and as a priority species in Annex II of the Habitats Directive (1992) (Casale & Tucker, 2015), and adjusted primarily due to threats, including habitat destruction, bycatch in fisheries, and climate change (Casale & Tucker, 2017b). Efforts to help the species' conservation are made globally, with various approaches such as the establishment of Marine Protected Areas (MPAs), the use of Turtle Excluder Devices (TEDs) in fisheries, and beach management practices that reduce human impact.

Identified nesting beaches often attract attention from environmental NGOs and local authorities, which help protect female turtles, their nests, eggs, and hatchlings (Lei & Booth, 2017; Stancyk et al., 1980; Talbert et al., 1980). Legal protections under the Endangered Species Act (ESA) (Valdivia et al., 2019) in the United States and the Convention on International Trade in Endangered Species (CITES) (Hill, 1990) regulate activities that impact sea turtles and their habitats (Mazaris et al., 2017). Efforts include establishing MPAs (Abalo-Morla et al., 2022; Scott et al., 2012; Wallace, DiMatteo, et al., 2010); beach patrols, and nest monitoring programs, often involving local communities and volunteers, focusing on community education and data collection (Marco et al., 2012); and regulating noise and light (Longcore & Rich, 2004) during the nesting season to reduce human impact.

In response to growing concerns about the impact of commercial fishing on vulnerable sea turtle populations, a specialized apparatus was designed to reduce the incidental capture of sea turtles in fishing operations, particularly in trawl nets (Jenkins, 2012; Kendall, 1990; Mitchell et al., 1995). Known as "Turtle Excluder Devices" (TEDs), these grid-like barriers allow smaller organisms, such as shrimp, to pass through into the net while directing larger animals, like sea turtles, toward an escape opening (Kendall, 1990). TEDs have evolved over the years increasing their effectiveness (Jenkins, 2012; Mitchell et al., 1995; Shiode & Tokai, 2004). Their efficiency has led to the widespread adoption of TEDs, promoting more sustainable fishing practices and contributing to the conservation of sea turtles and other species (Mitchell et al., 1995).

2. THE STUDY – EFFECTS OF ENVIRONMENTAL VARIABLES ON MORPHOLOGY AND FITNESS

2.1. Ideal Nesting Conditions

Ideal nesting conditions for sea turtles involve a combination of suitable beach characteristics and incubation conditions. Optimal beaches are typically sandy, with a gentle slope and minimal vegetation, allowing easy access for nesting females (Mortimer, 1990). Two factors that affect numerous aspects of embryonic development including embryo growth rate, sex, and hatching success are nest temperature and moisture content (Ackerman, 1994, 1996; Lolavar & Wyneken, 2020; Mcgehee, 1990). In loggerheads, optimal hatching success generally occurs when incubation temperatures are between 28.5°C and 31°C (Fisher et al., 2014; Usategui-Martín et al., 2019). Temperature limits vary by species and typically range from 25°C to 35°C (Howard et al., 2014b). Additionally, minimal human disturbance and low levels of artificial lighting are essential to prevent disorientation of both nesting females and emerging hatchlings, and proximity to the ocean is also important (Salmon & Witherington, 1995) to ensure hatchlings can quickly reach the water after emerging. These factors collectively contribute to successful sea turtle nesting and hatchling survival.

2.2. Environmental Variables

Hatchlings face numerous factors that influence their development and survival. Among these, temperature and inundation, directly affect hatching success, sex ratios, and overall population dynamics (Foley et al., 2006; Morreale et al., 1982).

Temperature plays an important role in determining the rate of embryonic development (Ackerman, 1996), affects hatching success, and influences sex determination in sea turtles, which exhibit temperature-dependent sex determination (TSD) (Morreale et al., 1982; Standora & Spotila, 1985). At low temperatures (26–28 °C), mostly males are produced; at intermediate temperatures (28–30 °C), both males and females are produced in roughly equal proportions;

and at high temperatures (30–34 °C), mostly females are produced (Yntema and Mrosovsky, 1982; Mrosovsky et al., 1985; Hewavisenthi and Parmenter, 2000).

For instance, lower temperatures that typically produce more males (Yntema & Mrosovsky, 1980) and slow down metabolic processes provide embryos with more stable conditions for development, resulting in larger hatchlings (Booth, 2017b; Herbert & Jackson, 1985). Whereas higher temperatures that generally produce more females (Yntema & Mrosovsky, 1980) and accelerate metabolic rates, potentially lead to faster development and smaller hatchlings (Booth, 2017b; Herbert & Jackson, 1985) but also increases the risk of anomalies or malformations (Martín-del-campo et al., 2021). With climate change, increased temperatures within the nest could therefore create a female bias, leading to a skewed sex ratio and potential reproductive challenges in the future s leading to a skewed sex ratio and potential reproductive challenges in the future (Fuentes et al., 2010; Hawkes et al., 2009; Telemeco et al., 2013)

Moisture content, particularly in species with permeable eggshells, regulates gas exchange and water balance within the embryo, making them highly susceptible to changes in water potential (Booth & Yu, 2009; G. C. Packard, 1999; M. J. Packard et al., 1982). Increased nest moisture content, resulting from sea level rise (SLR), storm events, and flooding, has been associated with longer incubation durations, reduced hatching success, larger hatchlings, and male-biased sex ratios (Ackerman, 1996; Caut et al., 2006; Foley et al., 2006; Howard et al., 2014b; Pike & Stiner, 2007). Adequate moisture levels prevent desiccation and maintain the necessary hydration for embryonic tissues, influencing development and overall viability (Mcgehee, 1990). Conversely, excessive moisture can hinder gas exchange, leading to hypoxia and developmental abnormalities (Mortimer, 1990; G. C. Packard, 1999).

The combined effects of temperature and moisture variability during incubation can also impact morphology and fitness traits such as growth rates, and locomotion (Gatto & Reina, 2020). Higher water content in the sand causes the sand temperatures to be lower than the surrounding air temperature (Sifuentes-Romero et al., 2018). Eggs in wetter substrates absorb significantly more water, but embryos develop more slowly in these cooler, moister conditions (Janzen et al., 1995; Staines et al., 2020). This slower development in moist, cool sand can have various

implications for the timing of hatching and overall survival rates, as embryos may take longer to reach maturity (Miller, 2017). Additionally, the thermal and moisture environment of the substrate can affect not only the rate of development but also the physiological traits of the emerging hatchlings, potentially influencing their adaptability in their natural habitats (Flores-Aguirre et al., 2023; D. W. Wood & Bjorndal, 2000).

2.3. Hatchling Fitness and Morphology

Environmental conditions during incubation, such as temperature and inundation, significantly influence the morphology and fitness of hatchlings (Booth et al., 2004; Flores-Aguirre et al., 2023). Higher temperatures may negatively impact overall hatchling size and strength, which can reduce their survival prospects (Staines et al., 2019). Inundation events during the nesting period can alter shell structure and limb development (Fleming et al., 2020), influencing a hatchling's buoyancy, agility, coordination, and overall physical endurance, impairing the hatchlings' ability to successfully navigate toward the ocean (Mickelson & Downie, 2010; Sim et al., 2015). Additionally, these environmental factors can influence muscle coordination and development, affecting self-righting and crawling abilities (Glen et al., 2003; Komara et al., 2023).

Hatchling mass and carapace size contribute to energy reserves and protection against predators (Miller, 2017), and are influenced by nest temperature and moisture levels, with higher incubation temperatures tending to produce smaller, lighter hatchlings (Booth et al., 2004; Flores-Aguirre et al., 2023; Staines et al., 2019). The size and shape of the carapace and plastron also affect buoyancy and stability in the water, contributing to a hatchling’s ability to avoid predators and reach feeding grounds (Bjorndal et al., 2000). Umbilical scar dimensions can indicate overall health and energy reserves, impacting the hatchling's initial survival in the marine environment (Bowen et al., 1995). Head and flipper size influence effective swimming and maneuverability (Salmon & Wyneken, 1987). Head size is affected by incubation temperature, with cooler temperatures potentially resulting in broader head widths, which are advantageous for feeding efficiency (Pilcher & Al-Merghani, 2000). Hatchlings with broader

heads and longer flippers generally exhibit better swimming efficiency and speed, enhancing their chances of survival during the early life stages (Pilcher & Al-Merghani, 2000).

Faster self-righting times and higher crawl speeds are associated with better survival rates, as they enable hatchlings to quickly orient themselves and move toward the ocean, thereby avoiding terrestrial predators and other hazards (Ischer et al., 2009; Salmon & Wyneken, 1987). Self-righting time and crawl speed depend on hatchling strength, energy reserves, limb development, and coordination, which are influenced by incubation conditions (Glen et al., 2003). Higher temperatures can impair muscle coordination, resulting in longer self-righting times and slower crawl speeds (Komara et al., 2023). Optimal nest temperature and moisture conditions lead to quicker self-righting times and faster crawl (Glen et al., 2003; Ischer et al., 2009, Komara et al., 2023).

3. BACKGROUND AND STATE OF OUR KNOWLEDGE

3.1. Current Knowledge

Sea turtle morphology, fitness, and environmental variables have been studied since the late 20th century (Chaloupka & Limpus, 1997; Miller, 1997). Early investigations examined species such as loggerhead, green, and leatherback turtles in nesting sites across the Americas and Australia (Bowen et al., 1993; Eckert & Eckert, 1988; Henwood & Ogren, 1987; Miller, 1997). Initial research explored how environmental factors like incubation temperature and moisture influence hatchling development and survival (Mcgehee, 1990; Miller, 1997). Subsequent studies expanded the scope to include additional environmental variables such as oxygen availability, nest microclimate, and sand grain size (Cheng et al., 2015; Erb et al., 2018; Foley et al., 2006; Lolavar & Wyneken, 2020; Mcgehee, 1990; Mortimer, 1990; Staines et al., 2019; D. W. Wood & Bjorndal, 2000). Ongoing research continues to refine our understanding of these environmental interactions and their effects on sea turtle hatchlings globally (Booth & Astill, 2001; Flores-Aguirre et al., 2023; Foley et al., 2006; Gatto & Reina, 2020; Laloë et al., 2017; Limpus et al., 2021; Mueller et al., 2019; Usategui-Martín et al., 2019).

Several studies have found that hatchlings from shaded nests exhibit faster crawl speed (CS) and self-righting time (RT) (Tables 1.1., 1.2., and 1.3.; Ischer et al., 2009; Rivas et al., 2019; Staines et al., 2019; A. Wood et al., 2014). This is likely due to the sub-lethal physiological effects of high temperatures in unshaded nests, where direct sun exposure increases nest temperatures (Bolten, 2003). Hatchlings from nests with high temperatures (>31 °C) have slower RT and CS compared to those from cooler nests (<31 °C) (Fleming et al., 2020; Kobayashi et al., 2017; Mickelson & Downie, 2010; Read et al., 2012; Seaman & Milton, 2023; Sim et al., 2015). However, an exception is noted in Fisher et al. (2014a), where nests with intermediate temperatures (28-30 °C) provided the best RT performance, and higher temperatures produced faster CS. Turtle eggs incubated at lower temperatures tend to produce male hatchlings with larger body sizes, including larger flippers (Booth et al., 2004; Burgess et al., 2006). Larger hatchlings not only improve fitness but also have a better chance of avoiding gape-limited predators (Burgess et al., 2006). However, the effects of moisture during incubation on the locomotor performance of sea turtle hatchlings are inconsistent. For most species, moisture does not significantly affect hatchling fitness (Gatto & Reina, 2020; Martins, Patino−Martinez, et al., 2022; Matthews et al., 2021). An exception is the flatback turtle, where higher moisture levels produce hatchlings with faster RT but no effect on CS (Gatto & Reina, 2020). In the case of the olive ridley turtle, higher moisture levels result in faster RT and CS, although these hatchlings were the slowest in the study(Gatto & Reina, 2020).

Morphological characteristics such as straight carapace length (SCL), straight carapace width (SCW), and flipper length (FL) also impact fitness performance (Tables 1.1., 1.2.). Some studies find that larger sizes lead to faster RT and CS (Fleming et al., 2020; Seaman & Milton, 2023), while others report that larger sizes result in slower RT and CS (Booth et al., 2013; Fleming et al., 2020; Martins, Patino−Martinez, et al., 2022).

Table 1.1. Literature review focused on temperature (T) as the primary environmental variable, examining its association with morphological variables—hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW), head width (HW), umbilical scar width (USW), umbilical scar length (USL), body depth (BD), flipper length (FL), and flipper width (FW)—to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Loggerhead turtle (*Caretta caretta*, Cc), Leatherback turtle (*Dermochelys coriacea*, Dc), Green turtle (*Chelonia mydas*, Cm).

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Loggerhead turtle (Cc)	Juno beach, Florida, USA 2018	15 N 144 H	No	Loggers	Mass, SCL, SCW, FL, USL, USW, BD	Bigger SCL slower RT; higher T slower RT	-	(Fleming et al., 2020)
Leatherback turtle (Dc)	Juno beach, Florida, USA 2019	12 N 115 H	No	Loggers	Mass, SCL, SCW, FL, BD	Bigger SCL, SCW, FL faster RT; higher T slower RT	No correlation between T and CS	(Seaman & Milton, 2023)
Leatherback turtle (Dc)	Pacuare beach, Costa Rica 2013-2015	144 N 1440 H	Yes Hatchery 800m	Shade, sun	Mass, SCL, SCW	2015 only; shade faster RT	shade faster CS	(Rivas et al., 2019)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2017-2018	12 N 120 H	Yes Same beach	Shade, sun	Mass, SCL, SCW	shade faster RT	shade faster CS	(Staines et al., 2019)
Green turtle (Cm)	Heron Island, Queensland, Australia 2008-2009	12 N 720 H	Yes North and south of the island	Loggers	Mass, SCL, SCW	Bigger carapace size slower RT	-	(Booth et al., 2013)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2009-2010	28 N 1120 H	Yes Same beach	No shade, least shade, intermediate shade, most shade	Mass, SCL, SCW	shade faster RT	shade faster CS	(Wood et al., 2014)
Loggerhead turtle (Cc)	Kochi beach, Japan 2015	6 N 351 H	Yes Same beach	Loggers	Mass, SCL, SCW	higher T slower RT	higher T slower CS	(Kobayashi et al., 2017)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2010-2012	44 N 1653 H	Yes Same beach	Loggers	Mass, SCL, SCW	higher T slower RT	higher T slower CS	(Sim et al., 2015)

Loggerhead turtle (Cc)	North Island, South Carolina, USA 2011-2012	3 N 99 H	Yes Lab - CMST, North Caroline	Incubator (27-32.5ºC)	Mass, SCL, SCW	middle T slower RT	higher T faster CS	(Fisher et al., 2014)
Leatherback turtle (Dc)	Turtle beach Stoneheaven beach, Tobago, Weast Indies 2008	16 N 107 H	Yes Same beach	Loggers	Mass, SCL, SCW, FL, FW, HW	-	higher T slower CS; smaller SCW and bigger FL faster CS	(Mickelson & Downie, 2010)
Green turtle (Cm)	Heron Island, Queensland, Australia 2006-2007	36 N 288 H	Yes Hatchery same beach	Shade, sun	SCL, SCW	-	shade faster CS; bigger size faster CS	(Ischer et al., 2009)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2011	20 N 2477 H	Yes Same beach	Loggers	Mass, SCL, SCW, FL	higher T slower RT; Mon Repos has faster RT	higher T slower CS; Mon Repos has faster CS	(Read et al., 2012)
	La Roche Percée, New Caledonia 2010	16 N 1997 H						

Table 1.2. Literature review focused on moisture (M) as the primary environmental variable, examining its association with morphological variables— hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW), head width (HW) and flipper length (FL)—to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Green turtle (*Chelonia mydas*, Cm), Flatback turtle (*Natator depressus*, Nd), Olive Ridley turtle (*Lepidochelys olivacea*, Lo), Loggerhead turtle (*Caretta caretta*, Cc)

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Green turtle (Cm)	Heron Island, Queensland, Australia	4 N 293 H	Yes Lab - Monash University, Melbourne	Induced: 4%, 6%, 8%	Mass, SCL, SCW, FL, HW	M didn't affect RT	M didn't affect CS	(Gatto & Reina, 2020)
Flatback turtle (Nd)	Curtis Island, Queensland, Australia	6 N 180 H				M at 6% and 8% faster RT (4%<6%=8%)	M didn't affect CS	
Olive Ridley turtle (Lo)	Tiwi Islands, Queensland, Australia	6 N 180 H				Higher M faster RT (4%<6%<8%)	Higher M faster CS; slowest hatchling	
Loggerhead turtle (Cc)	João Barrosa beach, Boa Vista Island, Cape Verde 2016-2018	279 N 5580 H	Yes Same beach	Natural: near shore, middle beach, dune vegetation	Mass, SCL, SCW	Bigger SCL slower RT; RT was similar across M zones	-	(Martins, Patino−Martinez, et al., 2022)

Table 1.3. Literature review focused on temperature (T) and moisture (M) as the primary environmental variables, examining their association with morphological variables— hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW) and flipper length (FL)— to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Green turtle (*Chelonia mydas*, Cm).

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Green turtle (Cm)	Kijal beach, Malaysia 2018	40 N 386 H	Yes Hatchery 48 km north	Temperature: Loggers Moisture: Induced (Low or high)	Mass, SCL, SCW, FL	-	No difference between M treatments; FL did not influence CS	(Matthews et al., 2021)

3.2. Knowledge Gaps

The existing literature underscores several significant gaps in understanding how environmental factors such as temperature and inundation affect sea turtle hatchlings. Most research has focused on single environmental variables, leaving a critical gap in the investigation of their combined effects (Tables 1.1., 1.2., and 1.3.). Current studies often examine the impacts of temperature or moisture in isolation, but there is a notable absence of research exploring how multiple interacting factors—such as temperature, moisture/inundation, sand type, and oxygen levels—affect hatchling fitness and morphology simultaneously (Fleming et al., 2020; Gatto & Reina, 2020). To address this gap, future research should aim to investigate these interactions within natural nest conditions. Conducting in situ studies is crucial, as relocating eggs to controlled environments can lead to complications or increased mortality (Ahles & Milton, 2016; Williamson et al., 2017).

Additionally, there is a need for comprehensive studies across all sea turtle species. The majority of existing research focuses on the loggerhead turtle (*Caretta caretta*) and the green turtle (*Chelonia mydas*), with relatively fewer studies on other species, such as the flatback turtle (*Natator depressus*), olive ridley turtle (*Lepidochelys olivacea*), and leatherback turtle (*Dermochelys coriacea*) (Gatto & Reina, 2020; Mickelson & Downie, 2010; Rivas et al., 2019). Each species may exhibit distinct morphological traits and fitness outcomes in response to environmental variables, accentuating the need for more inclusive research to better understand these species-specific responses and guide conservation efforts more effectively (Kobayashi et al., 2017; Mickelson & Downie, 2010; Staines et al., 2019).

Geographical variability also remains a significant knowledge gap. Most studies have been conducted in limited regions, such as Queensland, Australia, and Florida, USA (Tables 1.1. and 1.2.). There is insufficient data on how environmental factors impact hatchlings in diverse geographical locations with varying conditions (Gatto & Reina, 2020; Read et al., 2012). Expanding research to include multiple geographical regions is essential for understanding the variability of environmental factors and their potential impacts on hatchling development and fitness. This broader perspective will help to understand how regional differences influence

hatchling outcomes and inform region-specific conservation strategies (Kobayashi et al., 2017; Martins, Patino−Martinez, et al., 2022; Mickelson & Downie, 2010).

Furthermore, many studies have been limited to short-term observations within a single nesting season, lacking a longitudinal perspective (Fleming et al., 2020; Matthews et al., 2021; Read et al., 2012; Seaman & Milton, 2023). The impact of seasonal variability and long-term environmental changes on hatchling development remains poorly understood (Martins, Patino−Martinez, et al., 2022; Rivas et al., 2019; Sim et al., 2015). Longitudinal studies that span multiple nesting seasons are necessary to capture the full range of environmental variability and its effects on hatchling fitness and morphology (Rivas et al., 2019). Additionally, investigating how long-term climate changes—such as rising global temperatures and sea levels—affect sea turtle hatchling development and survival is fundamental for anticipating future challenges and informing adaptive conservation strategies (Fisher et al., 2014; Rivas et al., 2018; Williamson et al., 2017).

By addressing these knowledge gaps, future research can offer a more holistic view of the factors influencing sea turtle hatchling development and fitness. Such insights are important for developing targeted conservation strategies to mitigate environmental stressors and improve the survival of these endangered species.

4. OBJECTIVES

Several studies have investigated the effects of temperature and inundation (or moisture) on hatchling fitness and morphology, predominantly under controlled laboratory conditions or through nest/egg disturbances (such as transportation to a hatchery or laboratory, Tables 1.1, 1.2, and 1.3). However, understanding these relationships in natural, in situ incubation settings is essential, as this is their natural habitat. This study aims to help address this research gap by evaluating the combined effects of temperature, inundation, and morphology on the fitness of loggerhead hatchlings within their natural setting, without disturbing the nests or eggs or inducing temperature and inundation. The primary objectives are: (1) to advance our

understanding of how in situ incubation environmental conditions influence the fitness and morphology of hatchling loggerhead sea turtles (*Caretta caretta*), and (2) to investigate the impact of morphological characteristics on their fitness. Research questions 1 and 2 will address objective 1, while Research question 3 will focus on objective 2.

5. RESEARCH QUESTIONS AND HYPOTHESES

Research question 1: What are the impacts of temperature and inundation on the fitness of loggerhead sea turtle hatchlings?

Hypothesis 1: Loggerhead sea turtle hatchlings incubated at higher temperatures and subjected to periodic inundation will exhibit lower physical fitness. These conditions will result in slower crawl speeds and longer self-righting times. In contrast, nests incubated at optimal temperatures and without inundation will produce hatchlings with higher fitness levels, characterized by faster crawl speeds and shorter self-righting times.

Research question 2: What are the impacts of temperature and inundation on the morphology of loggerhead sea turtle hatchlings?

Hypothesis 2: Higher incubation temperatures and increased inundation are expected to reduce hatchlings' mass and size. On the contrary, lower incubation temperatures and no inundation will produce bigger and heavier hatchlings.

Research question 3: How do morphological characteristics influence the overall fitness of hatchlings?

Hypothesis 3: Among the morphological measurements of loggerhead sea turtle hatchlings—Mass, SCL, SPL, SCW, HW, USW, USL, and FL—hatchling mass, straight carapace length (SCL), and flipper length (FL) are expected to have the most significant influence on hatchling fitness. These characteristics will result in faster crawl speeds and shorter self-righting times in hatchlings with greater mass, longer SCL, and longer FL.

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Chapter II

Effects of *in situ* Incubation Environment on Hatchling Morphology and Fitness in the Northern Gulf of Mexico on Loggerhead Sea Turtles (*Caretta caretta*)

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Keywords: *Caretta caretta*, temperature, inundation, morphology, self-righting time, and crawl speed

ABSTRACT

Incubation conditions significantly influence various traits in reptilian neonates, a critical consideration for species like sea turtles. This study aims to understand how these conditions, particularly nest temperature and inundation, affect the morphology and fitness of loggerhead sea turtle (*Caretta caretta*) hatchlings. Temperature has been extensively studied among these conditions, revealing its profound effects on hatchling traits such as sex determination and growth rates. However, the role of nest inundation, which can also alter developmental outcomes, remains underexplored, despite its impact on hatchling size, sex, incubation duration, and hatching success. Previous studies often used relocated or laboratory-reared nests, which do not accurately reflect natural temperature fluctuations. To address this gap, we monitored in situ incubation conditions on St. George Island, Florida, during the 2022 nesting season by deploying temperature and water data loggers in seven loggerhead nests, although only data from four nests were usable for analysis. Upon hatchling emergence, eight morphological traits were measured, and fitness was assessed through self-righting time and crawl speed tests. Statistical analysis revealed that hatchling mass was a significant predictor of self-righting time, with heavier hatchlings taking longer to right themselves. Additionally, faster crawl speeds were associated with longer carapaces. Although temperature was not statistically significant, higher average temperatures were associated with slower self-righting time. Incubation at higher temperatures resulted in smaller and lighter hatchlings, consistent with previous studies, while inundation did not affect the morphology or fitness of hatchlings. These findings contribute to the existing knowledge of hatchling incubation effects, offering new insights into how regional environmental conditions influence hatchling development and fitness. However, the small sample size and focus on a single nesting season limit the generalizability of these results, suggesting a need for further research.

Keywords: *Caretta caretta*, temperature, inundation, morphology, self-righting time, and crawl speed

INTRODUCTION

Global climate change scenarios predict an increase in global mean air temperatures of 1.5°C by 2100, along with a heightened frequency of storms and extreme weather events (IPCC, 2023). These environmental changes pose significant threats to marine species, particularly those like sea turtles that rely on temperature and nest in coastal areas prone to inundation (Hawkes et al., 2009; Patrício et al., 2021a). Temperature plays an important role in determining the rate of embryonic development (Ackerman, 1996), affects hatching success, and influences sex determination in sea turtles, which exhibit temperature-dependent sex determination (TSD) (Morreale et al., 1982; Standora & Spotila, 1985). For instance, lower temperatures typically produce more males (Yntema & Mrosovsky, 1980) and slow down metabolic processes providing embryos with more stable conditions for development, resulting in larger hatchlings (Booth, 2017; Herbert & Jackson, 1985). Whereas higher temperatures generally produce more females (Yntema & Mrosovsky, 1980) and accelerate metabolic rates, potentially leading to faster development and smaller hatchlings (Booth, 2017; Herbert & Jackson, 1985) but also increasing the risk of anomalies or malformations (Martín-del-campo et al., 2021). With climate change, increased temperatures within the nest could therefore create a female bias in the primary sex ratio of some sea turtle populations and decrease hatchling mortality (Fuentes et al., 2010; Hawkes et al., 2009; Telemeco et al., 2013). Additionally, increased nest moisture content, resulting from sea level rise (SLR), storm events, and flooding, has been associated with longer incubation durations, reduced hatching success, larger hatchlings, and male-biased sex ratios (Ackerman, 1996; Caut et al., 2006; Foley et al., 2006; Howard et al., 2014; Pike & Stiner, 2007). Adequate moisture levels prevent desiccation and maintain the necessary hydration for embryonic tissues, influencing development and overall viability (Mcgehee, 1990). Conversely, excessive moisture can hinder gas exchange, leading to hypoxia and developmental abnormalities (Mortimer, 1990; Packard, 1999).

The combined effects of temperature and moisture variability during incubation can also impact morphology and fitness traits such as growth rates, and locomotion (Gatto & Reina, 2020). Higher water content in the sand causes the sand temperatures to be lower than the surrounding air temperature (Sifuentes-Romero et al., 2018). Eggs in wetter substrates absorb significantly

more water, but embryos develop more slowly in these cooler, moister conditions (Janzen et al., 1995; Staines et al., 2020). This slower development in moist, cool sand can have various implications for the timing of hatching and overall survival of eggs, as embryos may take longer to reach maturity (Miller, 2017). Additionally, the thermal and moisture environment of the substrate can affect not only the rate of egg development but also the physiological traits of the emerging hatchlings, potentially influencing their adaptability in their natural habitats (Flores-Aguirre et al., 2023; D. W. Wood & Bjorndal, 2000).

Environmental conditions during incubation, such as temperature and inundation, significantly influence the morphology and fitness of hatchlings (Booth et al., 2004; Flores-Aguirre et al., 2023). Higher temperatures may negatively impact overall hatchling size and strength, which can reduce their survival prospects (Staines et al., 2019). Inundation events during the nesting period can alter shell structure and limb development (Fleming et al., 2020), influencing a hatchling's buoyancy, agility, coordination, and overall physical endurance, impairing the hatchlings' ability to successfully navigate toward the ocean (Mickelson & Downie, 2010; Sim et al., 2015). Additionally, these environmental factors can influence muscle coordination and development, affecting self-righting and crawling abilities (Glen et al., 2003; Komara et al., 2023).

Several studies have demonstrated that hatchlings from shaded nests exhibit faster crawl speed (CS) and self-righting time (RT), likely due to the reduced sub-lethal physiological effects of high temperatures in shaded conditions (Ischer et al., 2009; Rivas et al., 2019; Staines et al., 2019; A. Wood et al., 2014). However, Fisher et al. (2014a) found that intermediate temperatures (28-30 °C) provided optimal RT performance, with higher temperatures enhancing CS. Hatchlings from lower-temperature nests tend to be larger, including having larger flippers, which can improve fitness and predator avoidance (Booth et al., 2004; Burgess et al., 2006). Moisture effects on locomotor performance are inconsistent across species, with some showing no significant impact (Gatto & Reina, 2020; Martins et al., 2022; Matthews et al., 2021), while others, like the flatback and olive ridley turtles, show enhanced RT and CS under higher moisture (Gatto & Reina, 2020). Morphological traits such as straight carapace length (SCL) and width (SCW) also impact fitness, though findings vary (Booth et al., 2013; Fleming et al., 2020; Martins, Patino−Martinez, et al., 2022; Seaman & Milton, 2023).

Most research focuses on single variables, overlooking the combined effects of temperature, moisture, sand type, and oxygen on fitness and morphology (Fleming et al., 2020; Gatto & Reina, 2020). Studies mainly target loggerhead and green turtles, neglecting other species like flatback, olive ridley, and leatherback turtles (Gatto & Reina, 2020; Mickelson & Downie, 2010; Rivas et al., 2019). Most studies have been conducted in limited regions, such as Queensland, Australia, and Florida, USA (Tables A1. and A2.), and often short-term, lacking insights into seasonal and long-term changes (Read et al., 2012; Rivas et al., 2019). Expanding to multiple regions and conducting longitudinal studies can improve our comprehensive understanding and effective conservation (Gatto & Reina, 2020; Martins et al., 2022).

Given the predicted increase in global mean air temperatures of 1.5°C by 2100, along with a heightened frequency of storms and extreme weather events (IPCC, 2023), it is important to establish how different environmental factors might affect hatchling morphology and fitness. Several studies have investigated the effects of temperature and inundation (or moisture) on hatchling fitness and morphology, predominantly under controlled laboratory conditions or through nest/egg disturbances (such as transportation to a hatchery or laboratory, Tables A1., A2. and A3.). However, understanding these impacts in natural, *in situ* incubation settings is essential, as it captures the variability of environmental parameters found in their natural habitat, unlike the controlled conditions of a laboratory. This study aims to help address this research gap by evaluating the combined effects of temperature, inundation, and morphology on the fitness of loggerhead hatchlings within their natural setting. The primary objectives are: (1) to advance our understanding of how *in situ* incubation environmental conditions influence the morphology and fitness of hatchling loggerhead sea turtles (*Caretta caretta*), and (2) to investigate the impact of morphological characteristics on their fitness.

To achieve these objectives, we collected data at St. George Island, Florida, USA, during the 2022 nesting season. This data included environmental variables such as temperature—average temperature during incubation (Temp), and the average temperatures for the first (T1), second (T2), and third (T3) thirds of the incubation period—and inundation parameters—inundation severity (I_S), frequency of inundation (I_F), and total inundation duration (I_D)—, as well as

detailed morphological measurements of hatchlings. The morphological parameters measured were hatchling mass, straight carapace length (SCL), straight plastron length (SPL), straight carapace width (SCW), head width (HW), umbilical scar width (USW), umbilical scar length (USL), and flipper length (FL). These variables were used to understand how environmental conditions and morphology affect the fitness of loggerhead sea turtle hatchlings—self-righting time (RT) and crawl speed (CS). St. George Island is a significant site for this study, as it hosts the largest loggerhead assemblage in the Northern Gulf of Mexico Recovery Unit (NGMRU) for loggerhead sea turtles (FFWCC, 2020).

MATERIAL AND METHODS

Study Area

This study was conducted on the ~20-kilometer public beach in Saint George Island (SGI), in Franklin County, Florida (Figure 2.1.). St. George Island hosts the largest loggerhead assemblage in the Northern Gulf of Mexico Recovery Unit (NGMRU) (FFWCC, 2020). The NGMRU spans beaches from the United States-Mexico border in Texas to Franklin Co., FL, and is a small (Ceriani et al., 2019; Silver-Gorges et al., 2021), genetically discrete subpopulation (Shamblin et al., 2012; Silver-Gorges et al., 2021) of the Northwest Atlantic Ocean Regional Management Unit (RMU) of loggerhead turtles (Wallace et al., 2010), the largest loggerhead RMU globally (Casale & Tucker, 2017; Ceriani et al., 2019). Nesting activities for the NGMRU typically occur from May to October (Ware et al., 2021).

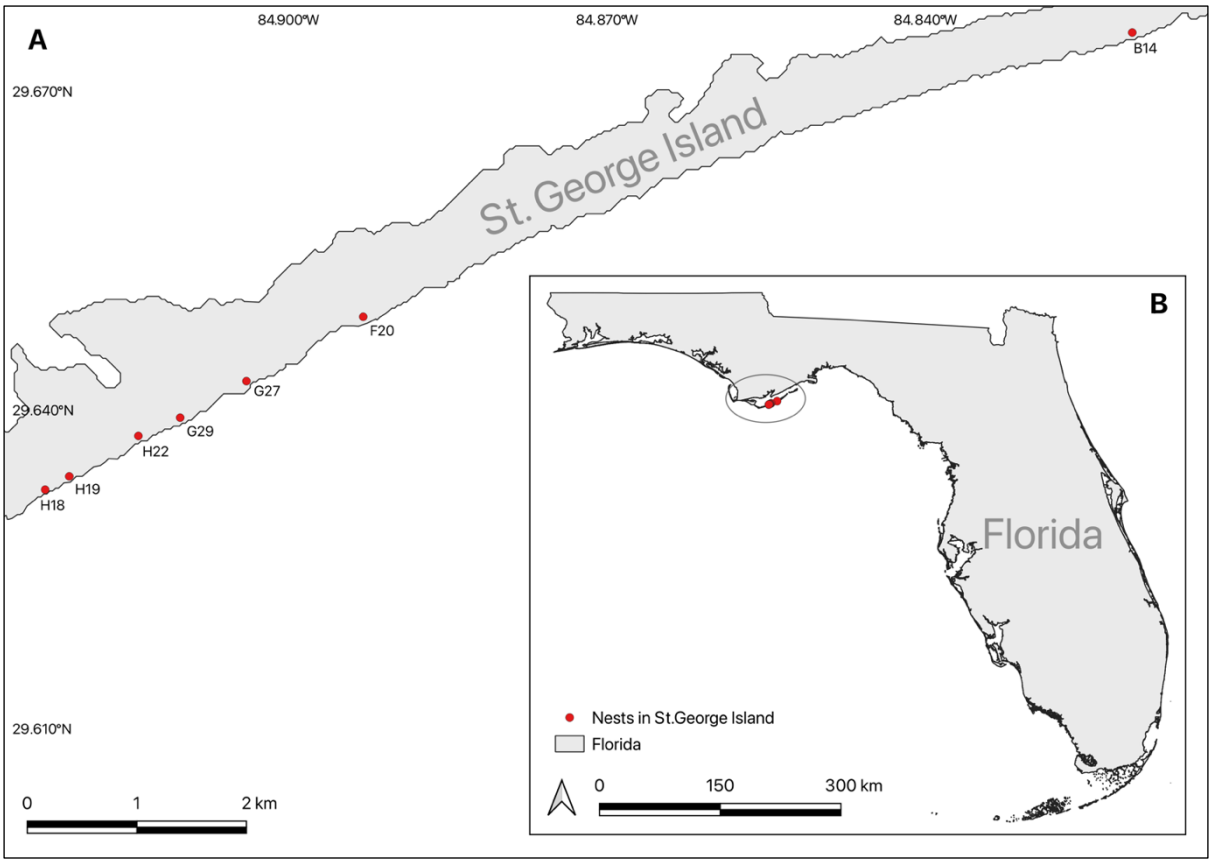

Figure 2.1. Location of the study site on St. George Island (A) in Florida (B), USA, within the Northern Gulf of Mexico Recovery region, indicating the location of sampled nests between June 19 and July 2, 2022.

Nest Monitoring

Loggerhead nesting activity was monitored during nightly beach surveys which took place over 2 weeks during the peak of the 2022 nesting season at SGI (Ingels et al., 2020), from June 19th to July 2nd. Encountered turtles were approached only after they had started covering their nests (or as they returned to the sea). All turtles were checked for pre-existing flipper or PIT tags, and they were applied when necessary. Morphometric data (curved carapace length (cm), notch to tip and notch to notch, and curved width (cm)) was collected during encounters with adult females, following protocols from the Florida Fish and Wildlife Conservation Commission Marine Turtle Conservation Handbook (FFWCC, 2016). The location of each nest was collected using a handheld Global Positioning System (Garmin 64s) and marked with stakes and flagging tape so that nests could be sampled when hatched.

Temperature loggers (HOBO Pendant UA-001-64, ONSET; Accuracy: ± 0.53°C from 0° to 50°C) were positioned in the approximate center of each nest (Tanabe et al., 2020), after the oviposition of ~50 eggs during the nesting process or in the morning by 9 am. Temperature readings (°C) were recorded at 30-minute intervals throughout the incubation period. Temperature data was categorized into four groups: the overall average temperature during incubation (Temp, ºC), and the average temperatures for the first (T1, ºC), second (T2, ºC), and third (T3, ºC) thirds of the incubation period for each nest.

Additionally, water loggers (HOBO Water Level Data Logger U20L, ONSET; Accuracy: ±0.3% FS, 0.62 kPa maximum error) were deployed adjacent to the nest at a depth of 60 cm, mimicking the bottom of the nest. The water loggers recorded absolute pressure every 30 minutes (Ware & Fuentes, 2018). All loggers were retrieved during nest inventories, either 3 days following hatching or 70 days post-oviposition. Inundation data was processed in HOBOware Pro ver. 3.7.26, where raw pressure readings were converted from kPa to meters (pressure depth) using the Barometric Compensation Assistant with data from the APCF1 station, Apalachicola, FL (NOAA, 2022). The processed inundation data was then analyzed in R, transforming the data into three inundation metrics: inundation severity (I_S, proportion) which quantifies the proportion of a nest affected by each inundation event, represented by the maximum inundation proportion observed for each nest. The frequency of inundation events (I_F, count) denotes the total number of inundation occurrences during the incubation period, and total inundation duration (I_D, h) refers to the cumulative duration, in hours, of all inundation events across the incubation period.

After 45 days of oviposition restraining cages were placed over the central region of each nest to restrain emerging hatchlings for morphological measurements and fitness tests. These cages were made from 0.6 cm mesh galvanized hardware cloth, measuring 60x60x60 cm as per the Florida Fish and Wildlife Conservation Commission Marine Turtle Conservation Handbook (FFWCC, 2016)

Hatchling Morphology and Fitness

After 45 days of incubation nests were checked three times per night to monitor for signs of hatchling emergency. Once the nest hatched up to 20 random hatchlings were selected for sampling from each nest. Hatchling mass (Mass, g) was determined on a digital scale. Straight carapace length (SCL, mm) and straight plastron length (SPL, mm) were measured from notch to notch. Straight carapace width (SCW, mm), head width (HW, mm), and umbilical scar width (USW, mm) were measured from the widest points of each respectively. Umbilical scar length (USL, mm) was measured from the top (closest to head) to the bottom (closest to tail) of the scar (Eckert et al., 1999). Flipper length (FL, mm) was measured by placing one front flipper of each hatchling next to a ruler and taking a photograph under a red light. The image was then put into ImageJ to determine the flipper length.

After the morphological measurements were collected, fitness tests were conducted. Self-righting time (RT, s) and crawl speed (CS, m/s) tests were performed for each selected hatchling as proxies for fitness (Fisher et al., 2014). Self-righting time was assessed by placing hatchlings onto their carapace, on flat sand, and the time (seconds) that hatchlings took to flip themselves upright, into a normal crawling position, was recorded (Gatto & Reina, 2020). Each hatchling was tested five times for a maximum of thirty seconds each. Directly after the self-righting tests, crawl speed was tested. For this test hatchlings were placed at one end of a 2.4-meter track that blocked external light and were guided using a white pen light, to simulate moonlight and stimulate the hatchling to crawl in that direction (Bourgeois et al., 2009). Each trial lasted for a maximum of five minutes for each of the two trials. The time taken for the hatchling to crawl from one end of the raceway to the other (including rests) was measured with a stopwatch and converted to crawl speed (m/s).

Data Analysis

Relationships between fitness, morphological, and environmental variables, as well as between morphological and environmental variables, were analyzed using linear mixed models (LMM) fitted by maximum likelihood in the R ‘lme4’ package (Bates et al., 2015), with ‘Nest ID’ was

used as a random effect to account for variability at the nest level. Within the environmental variables, all inundation variables were excluded from the initial full model by the linear mixed model program in R. The best-fitting model was selected using a combination of second-order corrected Akaike's Information Criterion (AICc), Bayesian Information Criterion (BIC), deviance, and log-likelihood (LogLik) scores (Burnham & Anderson, 2004). Additionally, the model's performance was evaluated using marginal R^2 (R^2m), which represents the variance explained by the fixed effects alone, and conditional R^2 (R^2c), which represents the variance explained by both the fixed and random effects (Nakagawa & Schielzeth, 2013). Models were ranked using the 'dredge' function from the R package 'MuMin' (Bartoń, 2023), which evaluates all possible models from a set of predictors. Models with delta (ΔAICc) values ≤ 4 were considered candidate models. The best-fitting model was then identified using the 'Anova' function with a chi-square test, comparing candidate models and the null model. All statistical analyses were performed using R software v.4.4.0 (The R Foundation for Statistical Computing, 2014) (R Core Team, 2024), assuming a 5% level of statistical significance. Normality was assessed using the Shapiro-Wilk test.

RESULTS

Seven nests were sampled, but information for all the variables considered was only obtained for four nests (F20, G27, G29, H22). This subset of nests comprised a total of 80 hatchlings, as detailed in Table 2.1. The remaining three nests, despite being sampled, did not provide sufficient data across all variables considered.

Table 2.1. Summary of sampled loggerhead turtle (*Caretta caretta*) hatchlings, showcasing average, standard deviation, minimum, and maximum values for each variable. Environmental variables include average temperature (Temp, ºC), temperatures during each third of the incubation period (T1, T2, and T3, ºC), inundation severity (I_S, proportion), frequency of inundation events (I_F, count), and total inundation duration (I_D, h). Morphological variables encompass hatchling mass (Mass, g), straight carapace length (SCL), straight plastron length (SPL), straight carapace width (SCW), head width (HW), umbilical scar width (USW), umbilical scar length (USL), and flipper length (FL), measured in millimeters, detailing phenotypical characteristics. Fitness variables include self-righting time (RT, s) and crawl speed (CS, m/s), describing locomotor efficiency. The inclusion of (-) indicates missing data for specific variables in certain nests.

Nest ID	B14	F20	G27	G29	H18	H19	H22	Average	Minimum	Maximum
Environmental variables										
Temperature (Temp, ºC)									24.35	34.06
Average	29.43	30.48	30.04	29.54	30.11	29.97	29.58	29.88		
Standard deviation	1.05	1.15	1.12	0.99	1.60	1.70	1.00	1.23		
First third of incubation (T1, ºC)	29.03	29.85	29.58	29.58	30.02	30.53	29.48	29.72	26.68	33.64
Second third of incubation (T2, ºC)	29.87	30.8	30.23	30.04	29.33	29.13	29.56	29.85	25.71	33.01
Third third of incubation (T3, ºC)	29.4	30.79	30.32	29.98	30.98	30.2	29.68	30.19	26.59	34.06
Inundation										
Severity (I_S, proportion)	-	0	0.896	1	0	0.058	0.648		0.001	1.00
Frequency of events (I_F, count)	-	0	1	2	0	16	1		1	16
Total duration (I_D, h)	-	0	1.5	7	0	72.5	1.5		0.5	11.0
Number of hatchlings	**20**	**20**	**20**	**20**	**15**	**20**	**20**			
Morphological variables										
Hatchling mass (Mass, g)									15.80	29.22
Average	21.18	20.18	20.22	21.39	25.77	-	17.62	21.06		
Standard deviation	0.52	0.56	0.56	0.93	1.52	-	0.80	0.82		
Straight carapace length (SCL, mm)									30.58	51.15
Average	45.67	45.08	46.71	45.75	45.13	42.27	42.73	44.76		
Standard deviation	0.82	0.96	0.82	1.72	4.90	1.27	1.06	1.65		
Straight plastron length (SPL, mm)									29.89	39.98
Average	36.22	35.91	35.89	36.42	34.33	31.56	32.90	34.75		
Standard deviation	0.64	1.58	1.07	1.59	3.10	1.54	0.64	1.45		
Umbilical scar length (USL, mm)									5.04	21.08
Average	10.26	8.42	7.82	11.06	14.84	7.45	7.16	9.57		
Standard deviation	0.82	1.25	1.06	1.28	4.62	1.40	1.02	1.64		
Straight carapace width (SCW, mm)									28.85	40.18
Average	34.28	33.92	34.82	34.63	35.48	32.22	32.39	33.96		
Standard deviation	0.75	1.21	0.68	2.13	2.60	1.00	1.13	1.36		
Head width (HW, mm)									8.35	20.91
Average	16.18	15.87	15.92	15.41	16.72	14.15	15.03	15.61		
Standard deviation	0.30	0.79	0.22	0.60	2.53	2.82	0.29	1.08		
Umbilical scar width (USW, mm)									2.46	18.68
Average	4.17	4.07	4.01	5.99	10.96	4.79	4.07	5.44		
Standard deviation	0.52	0.60	0.50	0.89	5.14	0.76	0.75	1.31		
Flipper length (FL, mm)									25.65	36.38
Average	32.46	32.45	32.09	30.91	28.50	31.00	30.00	31.06		
Standard deviation	1.29	1.72	1.94	2.13	1.78	1.88	1.83	1.80		
Fitness variables										
Self-righting time (RT, s)									0.85	30.00
Average	1.75	5.14	4.96	6.61	-	19.17	4.82	7.08		
Standard deviation	0.74	4.48	4.53	9.44	-	8.95	4.18	5.39		
Crawl speed (CS, m/s)									0.018	0.132
Average	0.086	0.055	0.071	0.075	-	0.041	0.053	0.06		
Standard deviation	0.019	0.012	0.013	0.019	-	0.015	0.010	0.01		

Nest temperature was obtained from seven nests (Table 2.1., Figure 2.2.). The overall average temperature was 29.88°C, ranging from 24.35°C to 34.06°C, with within-nest variations of ± 0.99°C to 1.7°C. The average temperature during each third of the incubation period varied from the nest's overall average temperature by ± 0.02ºC to 0.87ºC (Table 2.1.). Notably, nests H18 and H19 experienced significant temperature fluctuations, with peaks exceeding 33ºC on multiple occasions. In contrast, the other nests maintained more stable temperatures, remaining closer to the pivotal temperature, 29.2ºC (Woolgar et al., 2013) (Figure 2.2).

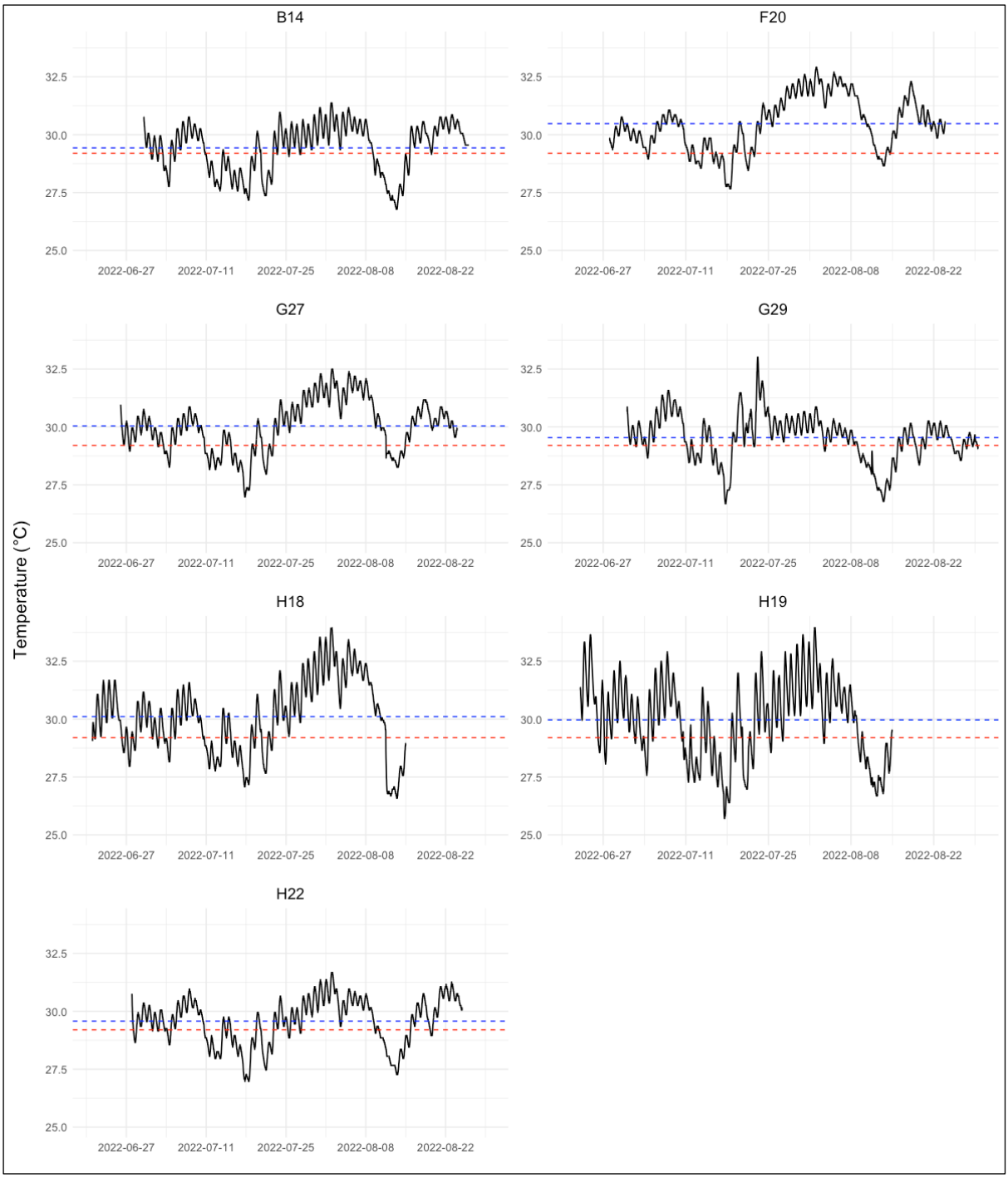

Figure 2.2. Temperature profiles for loggerhead nests monitored at St. George Island from June to August 2022. The dashed blue line indicates the average temperature of the respective nest and the dashed red line indicates the pivotal temperature for loggerheads, 29.2ºC.

Inundation data was collected from six nests (Table 2.1.), of these four were inundated during their incubation (Figure 2.3.). Nest G29 experienced the highest severity, and nest H18 experienced the lowest, measured as the proportion of the nest inundated. Nest H19 had the highest frequency of inundation events and the longest total duration of inundation, while nests

F20 and H22 had the shortest durations. Looking at the graphic representations (Figure 2.3.), there was a peak of inundation observed in nests G27, G29, and H22 on August 11th around 12:30 PM.

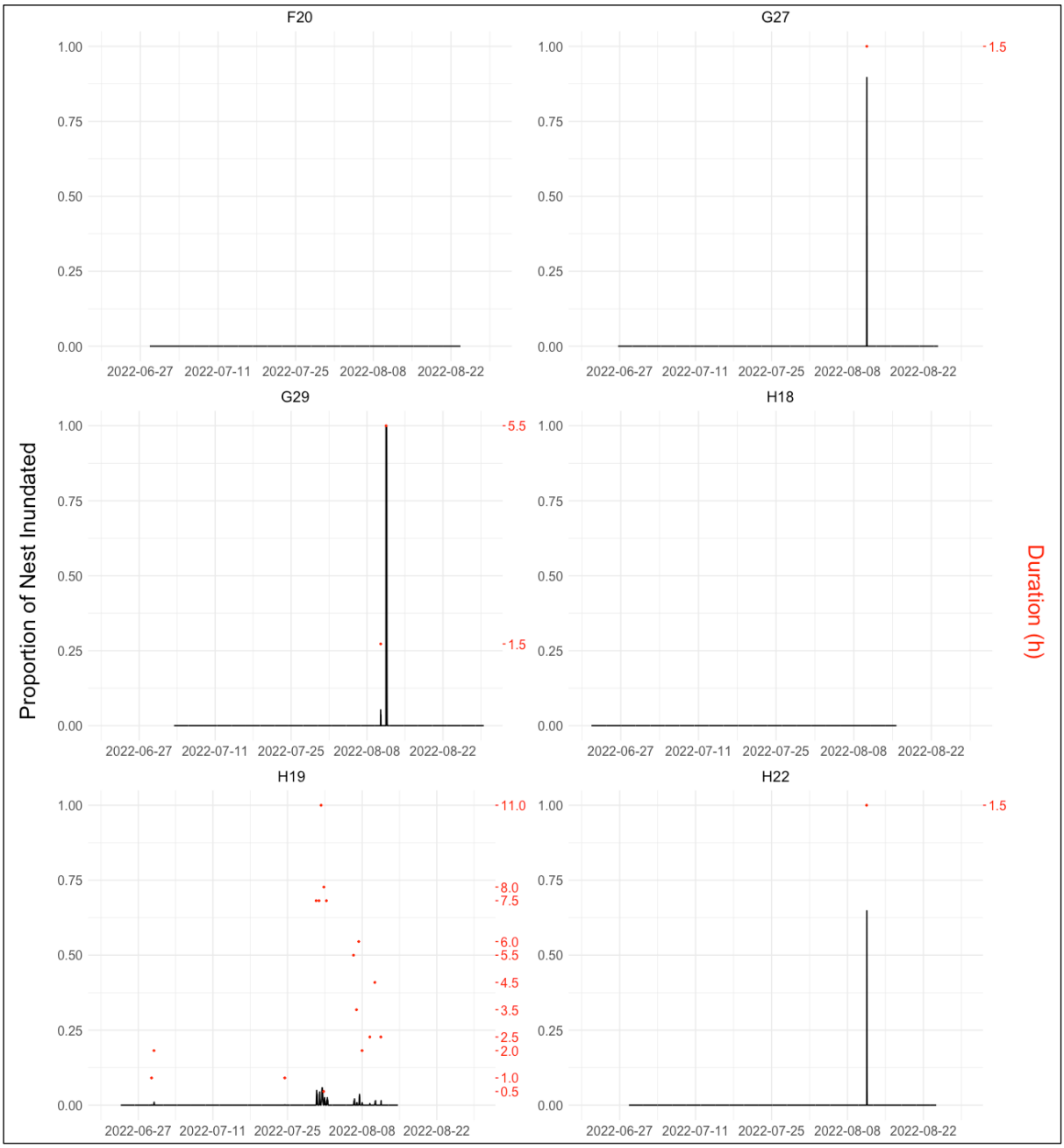

Figure 2.3. Inundation profiles were recorded and monitored from June to August 2022. The inundation severity (I_S) is measured as the proportion of nest inundated (left y-axis), occurrences in inundation activity represent the frequency of events (I_F), and the total duration of inundation (I_D, h) is the sum of each inundation duration (right y-axis). I_S and I_F are represented in black, while each inundation duration is represented in red. Notably, nests F20 and H18 did not experience any inundation. The highest proportion of nest inundation for nests

G27, G29, and H22 occurred on August 11th at approximately 12:30 PM, following a major wave washover event.

Hatchling measurements varied significantly between nests (Table 2.1., Figure 2.4.). The average mass was 21.06g ± 0.82g, nests H18 had heavier hatchlings, and H19 had lighter ones. SCL and SCW were fairly consistent, averaging 44.76mm ± 1.65mm and 33.96mm ± 1.36mm, respectively. SPL was shorter in nests H18, H19, and H22 compared to the overall average of 34.75mm ± 1.45mm, with H18 showing the most variation. USL and USW varied widely, particularly in H18, which had larger averages and a broader range. HW was similar overall (15.47mm ± 1.08mm), but H18 had larger heads and H19 had smaller heads. FL was generally consistent (31.06mm ± 1.80mm), except for H18, which had shorter flippers.

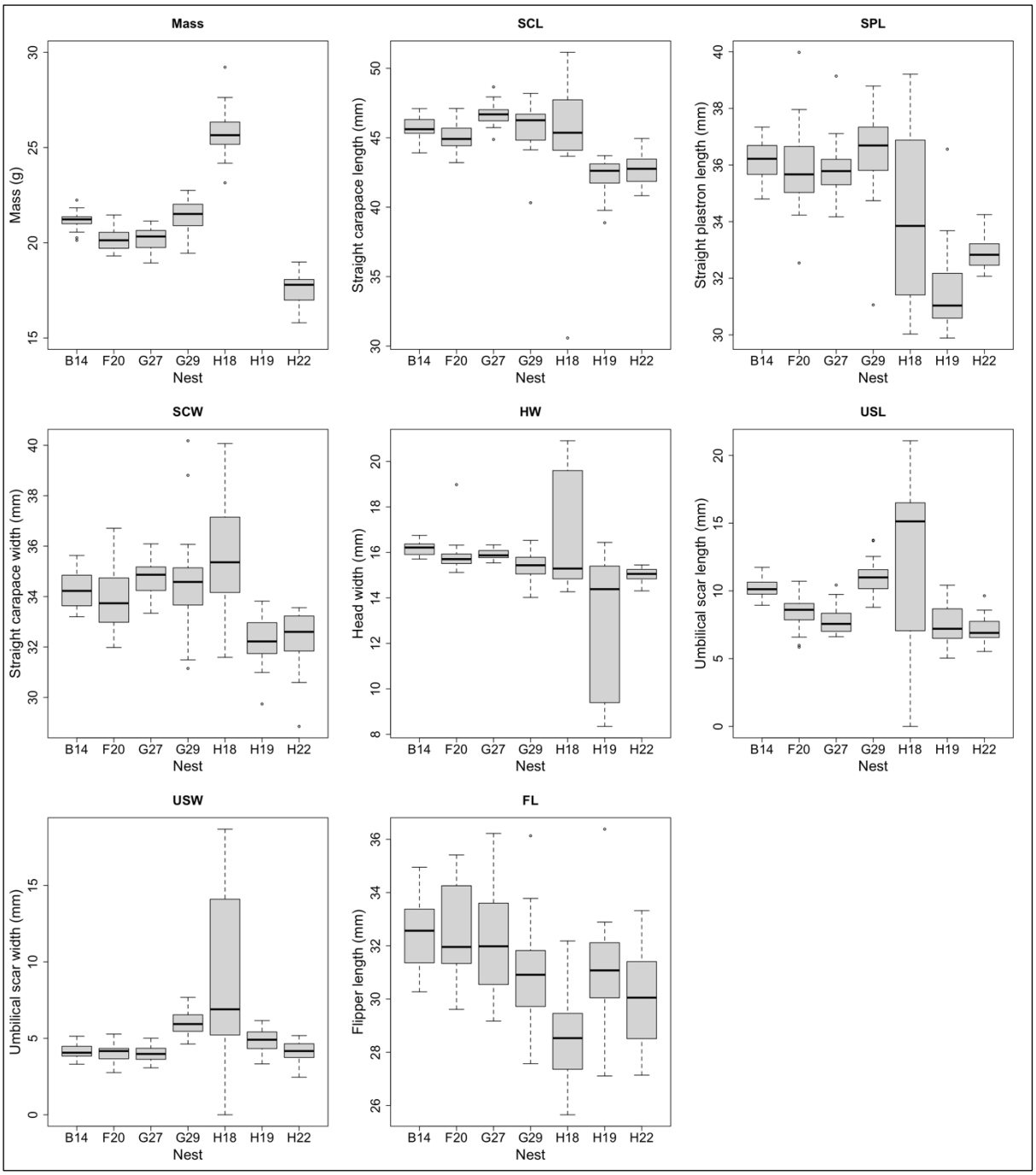

Figure 2.4. Mean, standard deviation, and range of hatchling mass (Mass, measured in grams), straight carapace length (SCL), straight plastron length (SPL), straight carapace width (SCW), head width (HW), umbilical scar width (USW), umbilical scar length (USL), and flipper length (FL), measured in millimeters, organized by nest.

Fitness variables indicated differences among nests (Table 1, Figure 5). Self-righting time (RT) ranged from 0.85s to 30.00s, averaging 7.08s ± 5.39s. Nest H19 had the most variation from 5.00s to 30.00s, and the longest average time (19.17s). Crawl speed (CS) ranged from 0.018

m/s to 0.132 m/s, averaging 0.06 m/s ± 0.01 m/s. In contrast to RT, nest H19 had the fastest hatchlings, averaging 0.041 m/s ± 0.015 m/s, with the fastest hatchling (0.018 m/s).

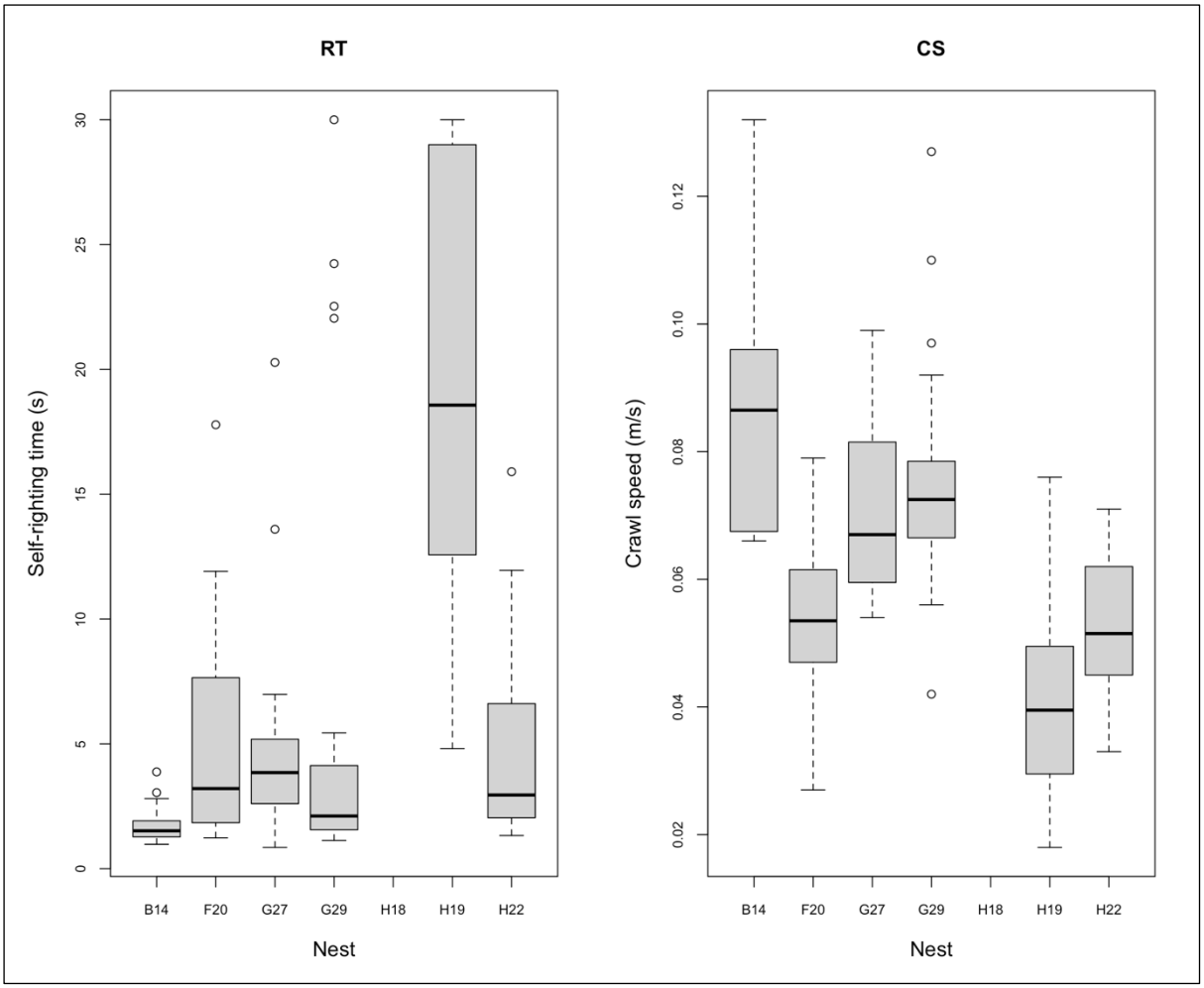

Figure 2.5. Mean, standard deviation, and range of fitness variables, encompassing self-righting time (RT, measured in seconds) and crawl speed (CS, measured in meters per second), organized by nest.

The statistical results concerning the relationships between our variables are summarized in Table 2.2. For fitness variables, mass was the only significant predictor for RT, with a positive effect (estimate = 2.424, $p = 0.012$). This indicates that heavier hatchlings took longer to right themselves. None of the other predictors, including SCL, HW, or temperature variables, had significant effects on RT. In contrast, CS was significantly influenced by SCL (estimate = 0.004, $p < 0.001$). Hatchlings with bigger carapace lengths had faster crawling. The models for RT and CS showed that temperature and inundation did not improve the fit of the model. Regarding morphological variables (Table 2.2.), Mass, SCL, SPL, SCW, and USL share the

same predictors (Temp, T1, and T2), and all models showed significant improvement over the null model, except USW (χ^2 = 0.974, p = 0.3237). However, within these models, none of the predictors, except for HW and FL, were statistically significant (p = 1). For HW, both predictors (T1 and T2) were statistically significant (T1: estimate = -4.244, p < 0.005; T2: estimate = 1.962, p < 0.001). A decrease in T1 and an increase in T2 were associated with an increase in HW. Additionally, FL was significantly influenced by T2 (Estimate = 4.169, p < 0.05), indicating that higher T2 temperatures were associated with increased flipper length.

Table 2.2. Summary of the best-fitted linear mixed-effects model and ANOVA analysis for various parameters (Fitness: RT, CS; and Morphology: Mass, SCL, SPL, SCW, HW, USL, USW, FL) against predictors (Morphology, Temperature: Temp, T1, T2, and T3, and Inundation: I_S, I_F, and I_D). Statistically significant results are marked with asterisks (* p < 0.05, ** p < 0.01, *** p < 0.001).

Parameter	Predictor	Estimate	Std. Error	df	t value	Pr(>|t|)	R^2m	R^2c	Chisq	Df	Pr(>Chisq)
RT	(Intercept)	189.900	518.900	0	0.366	1.000					
	Mass	2.424	0.940	73	2.577	0.0120 *					
	SCL	-1.069	0.583	73	-1.834	0.0707					
	HW	-1.679	1.280	73	-1.312	0.194	0.111	0.111	11.748	6	0.06783
	Temp	7.929	7.266	0	1.091	1.000					
	T1	-8.415	25.010	0	-0.336	1.000					
	T2	-4.847	11.740	0	-0.413	1.000					
CS	(Intercept)	-0.133	0.052	42	-2.568	0.013868 *	0.231	0.387	13.422	1	0.0002487 ***
	SCL	0.004	0.001	43	3.808	0.000441 ***					
Mass	(Intercept)	231.000	214100.00	0	0.001	1.000					
	Temp	-5.951	2582.00	0	-0.002	0.999	0.000	1.000	21.167	3	9.718e-05 ***
	T1	-10.960	10350.00	0	-0.001	1.000					
	T2	9.667	3502.00	1	0.003	0.998					
SCL	(Intercept)	554.000	765.800	0	0.723	1.000					
	Temp	-2.466	9.291	0	-0.265	1.000	0.175	0.886	7.289	1	0.006937 **
	T1	-26.500	37.030	0	-0.716	1.000					
	T2	11.600	12.530	0	0.925	1.000					
SPL	(Intercept)	256.700	388.500	0	0.661	1.000					
	Temp	-4.659	4.713	0	-0.989	1.000	0.336	0.718	11.799	1	0.0005927 ***
	T1	-12.490	18.790	0	-0.665	1.000					
	T2	9.549	6.358	0	1.502	1.000					
SCW	(Intercept)	335.900	633.500	0	0.53	1.000					
	Temp	-2.526	7.686	0	-0.329	1.000	0.104	0.783	6.257	1	0.01237 *
	T1	-15.470	30.630	0	-0.505	1.000					
	T2	7.691	10.370	0	0.742	1.000					
HW	(Intercept)	82.1016	30.0242	77	2.735	0.00775 **					
	T1	-4.2441	1.437	77	-2.953	0.00417 **	0.320	0.320	9.715	1	0.001828 **
	T2	1.9623	0.4451	77	4.409	3.33e-05 ***					
USL	(Intercept)	0.143	974.034	76	0.000	1.000					
	Temp	-9.035	11.817	76	-0.765	0.447	0.123	0.926	17.929	1	2.294e-05 ***
	T1	2.400	47.100	76	0.051	0.959					
	T2	6.884	15.941	76	0.432	0.667					
USW	(Intercept)	6.810	405.500	0	0.017	1.000					
	Temp	-5.151	4.920	0	-1.047	1.000	0.194	0.868	0.974	1	0.3237
	T1	1.867	19.610	0	0.095	1.000					
	T2	3.199	6.636	0	0.482	1.000					
FL	(Intercept)	117.729	108.511	77	1.085	0.281					
	T1	-7.159	5.194	77	-1.378	0.172	0.204	0.204	10.088	2	0.006448 **
	T2	4.169	1.609	77	2.591	0.0114 *					

DISCUSSION

Our study explored how temperature, and inundation, affect the morphology and fitness of loggerhead sea turtle hatchlings. We also investigated how hatchling's morphology influenced their physical fitness. We hypothesized that hatchlings that incubated at higher temperatures and subjected to periodic inundation would lead to reduced hatchling mass and size and exhibit lower fitness levels and that hatchling mass, straight carapace length (SCL), and flipper length (FL) would significantly influence fitness outcomes. Our results indicated that incubation temperature significantly affected morphological traits, including mass, straight carapace length (SCL), straight plastron length (SPL), and straight carapace width (SCW). Hatchlings incubated at higher temperatures tended to be smaller and lighter, these results align with previous laboratory and field-based research, which found that higher incubation temperatures lead to smaller hatchlings with shorter carapace lengths and lower masses (Booth & Astill, 2001; Fleming et al., 2020; Glen et al., 2003; Mickelson & Downie, 2010; Read et al., 2012; Sim et al., 2015). These studies also found that higher incubation temperatures resulted in smaller carapace lengths and lower hatchling masses. We found that hatchling mass was a significant predictor of self-righting time; heavier hatchlings took longer to right themselves. Other studies have looked separately at how temperature affects hatchlings' mass and their ability to right themselves, but no other study linked hatchlings' mass with their ability to right themselves. Additionally, crawl speed was significantly influenced by SCL, hatchlings with longer carapaces demonstrated faster crawl speed, consistent with previous studies (Dial, 1987; Staines et al., 2019), which emphasized the role of carapace length in terrestrial locomotion. Contrary to some research (Le Gouvello et al., 2020), FL was not a significant predictor of fitness in our study. While the effect of temperature on self-righting time was not statistically significant, we observed a trend of slower self-righting times at higher average temperatures, a finding in line with several locomotion studies (Booth et al., 2013; Booth & Evans, 2011; Burgess et al., 2006; Fisher et al., 2014; Fleming et al., 2020; Ischer et al., 2009; Sim et al., 2015), who reported that higher incubation temperatures negatively affected hatchling locomotor performance. Furthermore, the effect of inundation on both morphological and fitness variables was not statistically significant, indicating that periodic water exposure during incubation may not have the anticipated detrimental impact. However, the lack of significance could be attributable to the limited sample size, which may have constrained our ability to detect subtle effects.

Several limitations in our study should be acknowledged. The data was collected from only seven nests, with complete data available for only four, resulting in a small sample size that limits the generalizability of our findings. Additionally, the study was conducted over a short period during a specific period in a single nesting season, which may not capture the full variability of environmental conditions within and between seasons. The study's geographic limitation to St. George Island also restricts the applicability of our results to other locations. Furthermore, we did not account for other potential environmental and genetic factors, such as maternal effects and nest site characteristics, which could also influence hatchling fitness and morphology. Future research should aim to address these limitations by increasing the sample size and conducting long-term studies across multiple nesting seasons and sites. A more comprehensive analysis of the interactions between temperature, inundation, and other environmental factors could provide a deeper understanding of their combined effects on hatchling development. Additionally, experimental studies on other fitness variables, such as aquatic locomotion, could broaden the spectrum of fitness assessments. Incorporating genetic analyses and examining maternal effects would also enhance our understanding of their influence on hatchling fitness and morphology. Further exploration of inundation and moisture dynamics, including the frequency, duration, and severity of inundation events, could yield more nuanced insights into their specific effects. Expanding the study to include multiple nesting beaches with varying environmental conditions would allow for a comparison of results across different sites, and longitudinal studies could help monitor the long-term effects of incubation conditions on hatchling fitness and survival rates in the wild.

Climate change is impacting ecosystems globally, and sea turtles, being ectothermic organisms, are particularly vulnerable to these environmental shifts (Fuentes et al., 2011; Hawkes et al., 2009). Projections indicate that without effective intervention, sea turtle populations will experience a decline in effective population size (Hamann et al., 2010; Monsinjon et al., 2019). Rising incubation temperatures and sea level rise are just two of many climate change threats that will affect nesting beach habitats and the survival of sea turtles (Miguel et al., 2022; Patrício et al., 2021b). As these threats intensify, management strategies must adopt an integrative approach that combines various mitigation measures to address these complex and cumulative conservation challenges. This approach is essential for protecting sea turtles and their nests and

safeguarding the beaches on which their vulnerable embryos depend. This study contributes to the understanding of hatchling development by providing regional data on the effects of temperature and inundation on fitness and morphology, emphasizing the significant influence of incubation temperature on hatchling size and mass. Additionally, morphological traits such as hatchling mass and straight carapace length (SCL) were found to be correlated with key fitness traits—self-righting time, and crawl speed. Furthermore, by exploring the potential effects of inundation on hatchling fitness, we address a previously under-researched area, although our results suggest that inundation may not have a significant impact. Despite advances in the field, the need for continuous research remains, as further understanding of the environmental pressures affecting sea turtle populations is crucial for refining conservation strategies. Ongoing, comprehensive data collection on the ecological impacts of climate change is essential for developing effective measures that ensure the long-term survival and viability of these vulnerable species.

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Appendix

Table A4. Literature review focused on temperature (T) as the primary environmental variable, examining its association with morphological variables—hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW), head width (HW), umbilical scar width (USW), umbilical scar length (USL), body depth (BD), flipper length (FL), and flipper width (FW)—to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Loggerhead turtle (*Caretta caretta*, Cc), Leatherback turtle (*Dermochelys coriacea*, Dc), Green turtle (*Chelonia mydas*, Cm).

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Loggerhead turtle (Cc)	Juno beach, Florida, USA 2018	15 N 144 H	No	Loggers	Mass, SCL, SCW, FL, USL, USW, BD	Bigger SCL slower RT; higher T slower RT	-	(Fleming et al., 2020)
Leatherback turtle (Dc)	Juno beach, Florida, USA 2019	12 N 115 H	No	Loggers	Mass, SCL, SCW, FL, BD	Bigger SCL, SCW, FL faster RT; higher T slower RT	No correlation between T and CS	(Seaman & Milton, 2023)
Leatherback turtle (Dc)	Pacuare beach, Costa Rica 2013-2015	144 N 1440 H	Yes Hatchery 800m	Shade, sun	Mass, SCL, SCW	2015 only; shade faster RT	shade faster CS	(Rivas et al., 2019)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2017-2018	12 N 120 H	Yes Same beach	Shade, sun	Mass, SCL, SCW	shade faster RT	shade faster CS	(Staines et al., 2019)
Green turtle (Cm)	Heron Island, Queensland, Australia 2008-2009	12 N 720 H	Yes North and south of the island	Loggers	Mass, SCL, SCW	Bigger carapace size slower RT	-	(Booth et al., 2013)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2009-2010	28 N 1120 H	Yes Same beach	No shade, least shade, intermediate shade, most shade	Mass, SCL, SCW	shade faster RT	shade faster CS	(Wood et al., 2014)

Loggerhead turtle (Cc)	Kochi beach, Japan 2015	6 N 351 H	Yes Same beach	Loggers	Mass, SCL, SCW	higher T slower RT	higher T slower CS	(Kobayashi et al., 2017)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2010-2012	44 N 1653 H	Yes Same beach	Loggers	Mass, SCL, SCW	higher T slower RT	higher T slower CS	(Sim et al., 2015)
Loggerhead turtle (Cc)	North Island, South Carolina, USA 2011-2012	3 N 99 H	Yes Lab - CMST, North Caroline	Incubator (27-32.5ºC)	Mass, SCL, SCW	middle T slower RT	higher T faster CS	(Fisher et al., 2014)
Leatherback turtle (Dc)	Turtle beach Stoneheaven beach, Tobago, Weast Indies 2008	16 N 107 H	Yes Same beach	Loggers	Mass, SCL, SCW, FL, FW, HW	-	higher T slower CS; smaller SCW and bigger FL faster CS	(Mickelson & Downie, 2010)
Green turtle (Cm)	Heron Island, Queensland, Australia 2006-2007	36 N 288 H	Yes Hatchery same beach	Shade, sun	SCL, SCW	-	shade faster CS; bigger size faster CS	(Ischer et al., 2009)
Loggerhead turtle (Cc)	Mon Repos, Queensland, Australia 2011 La Roche Percée, New Caledonia 2010	20 N 2477 H 16 N 1997 H	Yes Same beach	Loggers	Mass, SCL, SCW, FL	higher T slower RT; Mon Repos has faster RT	higher T slower CS; Mon Repos has faster CS	(Read et al., 2012)

Table A5. Literature review focused on moisture (M) as the primary environmental variable, examining its association with morphological variables— hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW), head width (HW) and flipper length (FL)—to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Green turtle (*Chelonia mydas*, Cm), Flatback turtle (*Natator depressus*, Nd), Olive Ridley turtle (*Lepidochelys olivacea*, Lo), Loggerhead turtle (*Caretta caretta*, Cc)

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Green turtle (Cm)	Heron Island, Queensland, Australia	4 N 293 H	Yes Lab - Monash University, Melbourne	Induced: 4%, 6%, 8%	Mass, SCL, SCW, FL, HW	M didn't affect RT	M didn't affect CS	(Gatto & Reina, 2020)
Flatback turtle (Nd)	Curtis Island, Queensland, Australia	6 N 180 H				M at 6% and 8% faster RT (4%<6%=8%)	M didn't affect CS	
Olive Ridley turtle (Lo)	Tiwi Islands, Queensland, Australia	6 N 180 H				Higher M faster RT (4%<6%<8%)	Higher M faster CS; slowest hatchling	
Loggerhead turtle (Cc)	João Barrosa beach, Boa Vista Island, Cape Verde 2016-2018	279 N 5580 H	Yes Same beach	Natural: near shore, middle beach, dune vegetation	Mass, SCL, SCW	Bigger SCL slower RT; RT was similar across M zones	-	(Martins, Patino−Martinez, et al., 2022)

Table A6. Literature review focused on temperature (T) and moisture (M) as the primary environmental variables, examining their association with morphological variables— hatchling mass (Mass), straight carapace length (SCL), straight carapace width (SCW) and flipper length (FL)— to discern their impacts on fitness measures such as self-righting time (RT) and/or crawl speed (CS). Species: Green turtle (*Chelonia mydas*, Cm).

Species	Location/ year	Nests (N)/ Hatchlings (H)	Relocated (Yes/No)	Environmental variables	Morphological variables	Fitness results		Reference
						Self-righting time (RT)	Crawl speed (CS)	
Green turtle (Cm)	Kijal beach, Malaysia 2018	40 N 386 H	Yes Hatchery 48 km north	Temperature: Loggers Moisture: Induced (Low or high)	Mass, SCL, SCW, FL	-	No difference between M treatments; FL did not influence CS	(Matthews et al., 2021)

Table A4. Summary data on the frequency, severity, and duration of inundation events for different nests. Frequency (I_F, count) indicates the number of events observed. Severity (I_S, proportion) shows the proportion of severity for each event. Duration represents the duration of each event in hours. Total Duration (I_D, h) details the total duration of events in each nest. Some nests did not experience inundation, so their date and time entries are marked as (-).

Nest	Date	Time	Frequency (I_F, count)	Severity (I_S, proportion)	Duration	Total duration (I_S, h)
F20	-	-	0	0	0	0
G27	11/08/2022	13:00	1	0.896	1.5	1.5
G29	10/08/2022	12:30	2	0.053	1.5	7
	11/08/2022	12:30		1	5.5	
H18	-	-	0	0	0	0
H19	29/06/2022	11:30	16	0.001	1	72
	29/06/2022	22:30		0.01	2	
	24/07/2022	11:30		0.001	1	
	30/07/2022	08:30		0.049	7.5	
	30/07/2022	21:30		0.044	7.5	
	31/07/2022	07:00		0.058	11	
	31/07/2022	18:30		0.001	0.5	
	31/07/2022	19:30		0.025	8	
	01/08/2022	07:00		0.025	7.5	
	06/08/2022	09:00		0.021	5.5	
	06/08/2022	22:30		0.008	3.5	
	07/08/2022	08:30		0.036	6	
	07/08/2022	23:30		0.008	2	
	09/08/2022	10:30		0.005	2.5	
	10/08/2022	09:00		0.015	4.5	
	11/08/2022	12:00		0.015	2.5	
H22	11/08/2022	12:30	1	0.648	1.5	1.5