Ecology of sea turtles in the Chagos Archipelago, Indian Ocean

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Nesting green turtle returning to sea over the reef flat on Diego Garcia, Chagos Archipelago (Photo: Holly Stokes).

For my family

For your unconditional support, love and understanding

ABSTRACT

Understanding population size, distribution and reproductive success is vital for management and conservation planning. For rare and elusive species in remote island habitats, this information is difficult to obtain. As female sea turtles come ashore to nest, data can be collected relatively simply from the nesting population. Although other life stages are largely understudied, juveniles tend to forage at coastal sites and so in-water surveys can be conducted to estimate populations and study space use. To investigate aspects of sea turtle ecology in the remote islands of the Chagos Archipelago, Western Indian Ocean, I used a combination of traditional surveys and modern technology (remote and *in situ* sensing) to answer key questions relating to population size and threats to reproductive success. Most of my research focussed on nesting ecology including clutch incubation conditions, nesting behaviour, hatching success, and predation risk. To assess population size in remote areas, I experimented with *in situ* sensing (e.g., UAVs, camera traps) and validated results with traditional methods (e.g., foot patrols, in-water capture) to assess nesting and foraging populations. The findings demonstrate the novel approach of camera traps to successfully count turtle tracks and how the combination of UAV surveys, mark-recapture, and satellite tracking can effectively estimate immature turtle population densities. A wide range of sand temperatures were recorded spatially and temporally across the archipelago providing conditions for both male and female-biased clutches. To place my findings within a broader context, I conducted global meta-analyses and literature reviews, reporting the largest immature population of the critically endangered hawksbill turtle, and the first observations of coconut crab and invasive rat predation on sea turtle eggs. These results address several knowledge gaps about sea turtle ecology in the Western Indian Ocean, highlighting the importance of the Chagos Archipelago for all life stages and demonstrating complimentary tools for monitoring endangered species at remote locations.

DECLARATIONS AND STATEMENTS

Statement 1

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed: [redacted]

Date: 20/03/2024

Statement 2

This thesis is the result of my own investigation, except where otherwise stated. All other sources are acknowledged by footnotes giving explicit reference and a bibliography is appended.

Signed: [redacted]

Date: 20/03/2024

Statement 3

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

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Statement 4

This research has followed the University's ethical procedures and, where appropriate, ethical approval has been granted.

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Date: 20/03/2024

CONTENTS

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It is bittersweet to look back on the last four years and really take in the experiences I have gained, and lessons learned. What a rollercoaster ride of emotions and an incredible learning experience, not just in academia but in life. From starting the PhD in April 2020 as the pandemic took its toll on the UK, there have been times of real uncertainty for my fieldwork-based PhD, and extended periods of separation from family and friends. Yet, I have had some of the most inspirational, breathtaking, and beautiful moments of my life. I had huge support from so many people along the way but firstly I would like to start with my academic family and to thank my supervisor Dr Nicole Esteban for encouraging me as always through my MSc, PhD, and everything in between. Without you I am not sure I would have continued my academic journey. Thank you for believing in me and pushing me in the right direction when needed. We share incredible fieldwork memories from evening drives and saving coconut crabs, long nights patiently waiting for nesting turtles, my first experience satellite tagging and let's not forget sipping a beer to relax at the end of the week at the Yacht Club.

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They say you meet your lifelong friends during your PhD, and many of the amazing friendships throughout this journey were formed during my extended field trips in Diego Garcia. I am grateful to Milly, Elles, Taz, Lottie, Amanda, and Aska and so many more for your friendship, your incredible support in the field and for providing distractions through snorkelling, boat trips, and Yacht club Sundays. A big thank you to all of the volunteers that helped on island, and military personnel for fieldwork and logistical support. I am grateful to the Bertarelli Foundation for making this research possible through their generous support. Another special thank you to Josie Palmer, for being the best cabin mate, we were in the same boat literally and figuratively for parts of our lives and I appreciated your friendship and support.

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ETHICAL APPROVAL

All work was approved by Swansea University and Deakin University Ethics Committees and the British Indian Ocean Territory Administration (BIOTA) of the UK Foreign, Commonwealth and Development Office. Protocols were approved by research ethics committee of Swansea University (Ethics Reference Number: STU_BIOL_157334_011020182616_1; AWERB IP Reference Number: IP-2021-01). The study was endorsed through research permits (0006SE18, 0009SE18, 0004SE19, 0001SE21, 000XSE22) from the Commissioner's Representative for BIOTA and research complied with all relevant local and national legislation.

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LIST OF ABBREVIATIONS

A	Appendix
CCL	Curved Carapace Length
CCW	Curved Carapace Width
GIS	Geographical Information System
HWL	High Water Line
MHW	Mean High Water
MPA	Marine Protected Area
SCL	Straight Carapace Length
SCW	Straight Carapace Width
SD	Standard Deviation
SE	Standard Error
SI	Supplementary Information
TSD	Temperature-Dependent Sex Determination
UAV	Uncrewed Aerial Vehicle
VL	Vegetation Line
WIO	Western Indian Ocean

CHAPTER ONE: General Introduction

Sea turtles and population demographics

Sea turtles have complex life history patterns, which can vary between the seven species, but follow the pattern of oviposition and embryo development in terrestrial habitat on sandy beaches and foraging in the open ocean and coastal waters (Bolten 2003). Mating is thought to predominantly occur in the region of the nesting site, and females come ashore to lay multiple clutches of hundreds of eggs during a nesting season (Miller 1997). Depending on species and sand temperature, eggs incubate for ~50-70 days (Ackerman 1981; Booth 2017) before hatchlings emerge and crawl to the sea. At this stage, hatchlings are at high risk of predation (Fowler 1979). However, if successful in crawling the beach and crossing over the reef, they head to the open ocean where they spend an unknown period of time (often termed the 'lost years') before returning to neritic habitat to complete development to sexual maturity (Musick and Limpus 1997). Sea turtles also display temperature dependent sex determination (TSD), whereby the sex of hatchlings is determined by the temperature of the sand and so climate change related rising temperatures are of concern (Standora and Spotila 1985).

Habitat preferences and feeding strategies differ between species.In general, green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) turtles follow the oceanic to neritic pattern undergoing an ontogenetic shift in habitat (Arthur et al. 2008; Avens et al. 2021) and in diet in the case of green turtles where they are reported to shift from an omnivorous diet in oceanic habitats to an herbivorous diet, predominantly consisting of seagrass in coastal habitats (Howell et al. 2016; Burgett et al. 2018). As green turtle diet is known to vary ontogenetically (Howell et al. 2016), by habitat, and regions (Santos et al. 2015) and so we explored these variations further and assessed the influence of sea surface temperature on their diet in a global review (chapter two).

Understanding population size, distribution and reproductive success is essential for management planning. However, for elusive species, population estimates, and ecological information is difficult to obtain, particularly at remote habitats (Mcdonald 2004). Sea turtle research is often focussed on adult females as they come ashore to nest and information can be obtained from individuals, their tracks, and nests (Mazaris et al. 2017). Less is known about the juvenile life stage (Wildermann et al. 2018), although when juveniles shift to neritic habitat in shallow waters, in-water surveys can be conducted to further our understanding of this life stage (Strindberg et al. 2016). To assess population growth or decline, several parameters are important to understand including population size, growth rates, sex ratios, and fecundity (Piacenza et al. 2016).

Globally, green turtles are listed as endangered (Seminoff 2023) and hawksbill turtles as critically endangered (Mortimer and Donnelly 2008) on the IUCN red list. Like other regions, the conservation status for the green turtle subpopulation in the Southwest Indian Ocean has recently been downlisted to Least Concern (Bourjea and Dalleau 2023). The growing evidence for increasing population trends across species and regions is likely due to conservation efforts around the world (Hays et al. 2024). Despite conservation success stories, turtles face an array of threats across all life stages including direct harvesting, habitat loss, fisheries bycatch, climate warming, and predation (Donlan et al. 2010).

Threats to sea turtle eggs

Offspring survival rate is a key demographic factor that drives population success and for many decades the assessment of factors driving survival has been a vital component of ecological studies (Gibson et al. 2017; Reglero et al. 2018). Sea turtles produce hundreds of eggs per clutch, and lay several clutches per nesting season (e.g., Hays and Speakman 1991). They provide no parental care for their offspring beyond selecting suitable nest sites for embryo development (e.g., away from the sea to minimise sea water inundation; Patrício et al. 2018) and the eggs are at risk of fungal infection (Chai et al. 2023), poaching (Poti et al. 2021), predation (Leighton et al. 2011), warming sand temperatures (Laloë et al. 2014) and inundation (Pike et al. 2015).

Temperature

Temperature plays a key role in the development of animals (Lillie and Knowlton 1987). For sea turtles, that bury and incubate their eggs in the sand, sand temperature directly affects the duration of incubation (Booth 2017), hatchling sex ratios (Santidrián

Tomillo and Spotila 2020), embryo survival (Howard et al. 2014), hatchling emergence patterns (Drake and Spotila 2002), and hatchling performance (Booth 2017). As sea turtles exhibit temperature dependent sex determination (TSD), whereby fewer males and more females are produced at warmer incubation temperatures, climate warming is of concern (Santidrián Tomillo and Spotila 2020). Sand temperatures are influenced by several factors including seasonal patterns and changes in weather (Mrosovsky et al. 1984), sand albedo (Hays et al. 1995), level of shading (Wood et al. 2014), and beach orientation (Esteban et al. 2018a). Sand temperatures at sea turtle nesting beaches have been studied widely around the world (e.g., Raine Island, Australia, Booth et al. 2020; Ascension Island, central Atlantic, Godley et al. 2002; Cape Verde Islands, North Atlantic, Laloë et al. 2017), and high spatial and temporal variation has been reported from sand temperatures predicted from mechanistic models (Bentley et al. 2020). Given our long-term (decade) sand temperature recordings across nesting beaches in the Chagos Archipelago, we were able to explore the spatial and temporal variations in sand temperatures using empirical data and highlight the value in understanding the temperature variability at a site when modelling the effects of temperature on hatchling sex ratios (Chapter four).

Sea level rise

As a result of climate warming, and a concern for sea turtles is the influence of rising sea levels on the availability of nesting habitat (Rivas et al. 2023). Most sea turtle species aim to crawl an adequate distance away from the sea to minimise nest inundation (Martins et al. 2022a) and sometimes that results in nesting under vegetation at the back of the beach already at the extremes of available nesting habitat. For example, leatherback turtle (*Dermochelys coriacea*) nests are most at risk of saltwater flooding as they are often laid in open areas of the beach close to the sea (Mrosovsky 1983; Rivas et al. 2018), whereas green and hawksbill turtles often choose nest sites further up the beach close to vegetation if present (Serafini et al. 2009; Patrício et al. 2018). Rivas et al. (2023) assessed the effects of sea level rise using Intergovernmental Panel on Climate Change (IPCC) scenarios on sea turtle nests of five species at seven nesting rookeries around the world. Predictions reported include 100 % nest flooding under moderate emissions scenarios for 2050 at Raine Island, Australia and Soana Island, Dominican Republic. Hence, nest site selection is particularly important to study on low lying atolls with narrow beaches (Rivas et al. 2023), like the index beach on Diego Garica, Chagos Archipelago where nest site selection has not previously been studied (Chapter three).

Predation

Additionally, offspring survival can be heavily affected by predation of sea turtle eggs from naturally occurring predators, for example, raccoons (*Procyon lotor*) in Florida, or invasive predators that can further increase mortality for example, feral pigs (*Sus scrofa*) in Trindade Island, Brazil (Pereira et al. 2023). In the Chagos Archipelago, hatching success, including rates of predation on sea turtle eggs has not previously been researched. We add to the extensive list of species reported to feed on sea turtle eggs around the world by adding two previously unreported predators, one invasive and one native species (Chapter Five).

Using remote and in situ sensing technology to facilitate sea turtle research

Although data collection is relatively simple for adult females, and for juveniles in coastal waters compared to other life stages, many sea turtle populations nest and forage within remote habitats and knowledge gaps persist at these often dangerous or logistically difficult to access sites (Whiting et al. 2014; Mortimer et al. 2020). Given the need to assess populations that inhabit remote locations and the availability of remote and *in situ* sensing technology, it is not surprising that new devices play a role in increasing our understanding of animals and their ecology (Marvin et al. 2016). For example, satellite tracking has been used to assess clutch frequency (Esteban et al. 2017), UAV (Uncrewed Aerial Vehicles) surveys for population estimates of nesting turtles (Dunstan et al. 2020) and remote satellite imagery to count turtle tracks (Casale and Ceriani 2019). Additionally, the concept that a combination of traditional (e.g., ground surveys) and remote and *in situ* sensing technology can complement and enhance data quality is increasingly acknowledged in conservation (Zwerts et al. 2021).

In recent years camera traps have been incorporated into sea turtle research to investigate predation of nesting turtles (Fonseca et al. 2020), nests (Lei and Booth 2017b) and hatchlings (Gronwald et al. 2019). Predator behaviour patterns and strategies for nest protection have also been assessed using camera traps (Guilder et al. 2015; Lovemore et al. 2020). Expeditions to the Chagos Archipelago are usually restricted to one per year for roughly four to five weeks and so the temporal coverage of the green and hawksbill nesting season at this site is limited. To increase temporal coverage for nesting population estimates in the Chagos Archipelago, we explore the use of camera trapping technology with traditional foot patrols as a new methodological approach (Chapter six). We also explore the combination of two modern techniques (satellite tracking and UAV surveys) and traditional mark-recaptures for immature abundance estimates (Chapter seven). An important question raised is what are the impacts of such devices on the animals? Negative effects have previously been reported including UAV disturbance to wildlife (Mulero-Pázmány et al. 2017) and growth reduction in tagged Atlantic Salmon, *Salmo salar,* likely due to drag (Hedger et al. 2017). Hence, given the opportunity to remove satellite tags from immature turtles at our study site led to the assessment of the effects (through growth rate comparisons) from satellite tags (chapter eight).

The importance of the Chagos Archipelago for sea turtles

The Indian Ocean is often referred to as the least explored ocean, particularly the Western Indian Ocean (WIO; Hood et al. 2016). Sea turtle research in the Chagos Archipelago was initiated in 1970 where interviews with inhabitants across some islands indicated just a few hundred annual nesting green and hawksbill turtles (<1000 annual clutches laid; Frazier et al. 1975). In 1996, Mortimer and Day 1999, expanded on these findings and led the first systematic snapshot survey of nesting turtles across the archipelago and estimated 400-800 green (2200-4400 clutches) and 300-700 hawksbills (1200-2800 clutches) annually. A further update of estimates show that the archipelago provides nesting habitat for 39-51% of an estimated 12,500-16,000 hawksbill and 14-20% of an estimated 104,000-143,500 green turtle clutches laid throughout the south-west Indian Ocean (Mortimer et al. 2020). Increasing nesting numbers has been attributed to > 40 years without significant exploitation from humans and the no-take 640,000 km^2 Marine Protected Area (MPA; Koldewey et al. 2010) created in 2010 which encompasses nesting beaches on over 55 islands in the archipelago. Furthermore, the MPA provides protection of foraging sites for juvenile green and hawksbill turtles in

Diego Garcia (Hays et al. 2021a) and seagrass habitat for adult green turtles, including the Great Chagos Bank (Esteban et al. 2018).

Through satellite tracking of green turtles from their nesting beach on Diego Garcia to their foraging sites, studies have shown the importance of this nesting site as a refuge, providing beaches for turtles that forage in the Chagos Archipelago as well as the wider WIO, ranging from the Republic of Seychelles to Somalia and southward to Madagascar and Mozambique (Hays et al., 2014; Hays et al. 2020). Moreover, another important factor regarding nesting beaches in the Chagos Archipelago is that sand temperatures are relatively cool revealing balanced sex ratios of 53% hawksbill and 63% green male hatchling production (Esteban et al. 2016), compared to nesting sites with high sand temperatures and female-biased sex ratios. For example, at Raine Island, Australia, Booth et al. 2020, where recorded nest temperatures were on average 30˚C during the first week of incubation and estimated only 0.7% of green turtle hatchlings were male over an entire nesting season.

There are fewer studies focussed on the immature life stage and development habitat in the Chagos Archipelago. Recent research conducted at Turtle Cove, Diego Garcia, showed differences in space use for immature turtles but found many displayed high fidelity to very small areas (Hays et al. 2021a). Long-term monitoring of the immature turtle population at Turtle Cove has been ongoing since 1996 (Mortimer and Day 1999) and there are studies in line to further understand the demography of this population, as well as expanding further afield to developmental habitats on the oceanside of Diego Garcia and wider Chagos Archipelago.

Due to the remoteness of the Chagos Archipelago, most findings are the results of expeditions spanning no more than two months, with often little opportunity to visit the outer islands of the archipelago and so there is limited temporal and spatial coverage in this region. However, environmental personnel of the US Navy Support Facility were able to assist and conduct monthly track surveys (March 2006-April 2007; April 2011-May 2013; November 2014-March 2018) at the index beach on Diego Garcia and these surveys were used to define nesting seasonality for both species finding that green turtles nest year-round with a peak between June and August, and hawksbills nest between October and February (Mortimer et al. 2020). Understanding the nesting seasonality was vital for my PhD expedition planning to study sea turtle nesting ecology, particularly hatching success, predation risk, and nesting behaviour.

Aims

The aim of this thesis was to conduct fieldwork across the nesting season, from egg laying to hatching, to assess nesting behaviour (e.g., nest site selection), incubation conditions (e.g., sand temperature) and to monitor the incubation period to investigate hatching success, and predation risk. These areas of research were motivated by knowledge gaps due to previous limitations on the duration of expeditions in the Chagos Archipelago. Additionally, we aimed to assess the use of remote and *in situ* sensing technology (e.g., UAVs, satellite tracking and camera trapping) alongside traditional techniques (e.g., foot patrols, capture-mark-recapture) to facilitate our research and improve spatial and temporal coverage. The following objectives were identified to achieve the theses aims:

1. Night and day-time surveys on the Index beach, Diego Garcia, Chagos Archipelago:
    - Hatching success: Locate and observe nesting females for clutch counts and mark and re-locate nests for nest inventories to assess the number of eggs laid and the number of eggs successfully hatched, including the number of eggs predated in the nest to calculate predation rates. Monitor (via observations on foot-patrol surveys and surveillance camera set up) nests for hatchling emerge to identify the main nest predators.
    - Nest site selection: Locate and observe nesting females to record nest locations and assess nest site selection in relation to vegetation, high water line, and the sea.
2. Daytime survey on the Index beach, Diego Garcia, Chagos Archipelago:
    - Set up camera traps facing down the beach taking photographs at sunrise to capture turtle tracks in the sand.
    - Foot patrol surveys to count green and hawksbill tracks, false crawls and nests.
3. Daytime surveys in Diego Garcia and outer islands in the Chagos Archipelago:

    - Deploy temperature loggers in the sand to record temperature in different nesting habitats, sites along the beach and islands.
    - Spot sand temperature measurements using a temperature probe in different nesting habitats, sites along the beach and islands.
4. Daytime surveys at Turtle Cove, Diego Garcia, Chagos Archipelago:
    - Immature turtle abundance estimates: Capture immature hawksbill and green turtles, measure turtle length and width, mark turtles with non-toxic white paint, and release the turtles. Conduct drone flights to resight and count marked and unmarked turtles to calculate the abundance of turtles at an important foraging and developmental habitat.
    - Effects of satellite tagging: Capture satellite tagged turtles and remove satellite tags to assess the attachment site for damage. Measure turtle length post satellite tag removal. Calculate growth rates of tagged and untagged individuals to compare growth rates between the two groups to assess whether satellite tagging affected the growth rates of immature hawksbill turtles.

Thesis presentation

I present my thesis as seven research papers (four published, two submitted, and one as a manuscript in preparation). All contributions from my supervisors and co-authors for each chapter are described on the title page of each chapter. Published chapters have been reformatted specifically for this thesis in the style of Marine Biology.

Research approach

The main theme of my thesis was to understand sea turtle ecology in the Chagos Archipelago using a combination of novel and traditional techniques, including UAV surveys, capture-mark-recapture, foot patrol track surveys, environmental sensors (e.g., temperature probe, buried temperature loggers), satellite telemetry, surveillance cameras (monitoring nests) and camera traps. My research mainly focussed on nesting ecology, including nest site selection of green turtles on Diego Garcia and globally, incubation conditions (temperature) across the Chagos Archipelago, and predation of green turtle eggs in Diego Garcia and globally.

Initial plans for PhD research included a research focus on the nesting ecology of both green and hawksbill turtles, however, my PhD commenced in April 2020 during a series of COVID-19 lockdowns and so my fieldwork was delayed by 6-months, and I was unable to visit field sites during hawksbill turtle nesting season. Therefore, my research took a slight turn initially where my focus was re-directed to participation in a global green turtle diet study and UAV video analysis. The UAV video analysis led to a study on population abundance of immature green and hawksbill turtles in Turtle Cove, Diego Garcia by combining UAV surveys, mark-recapture, and satellite tracking. During the mark-recapture study in the shallow lagoon, there were opportunities to remove satellite tags that had been attached to turtle carapaces during 2018-2019 and so I was able to assess the growth rate and condition of turtles post tagging, leading to an additional chapter on the effects of satellite tagging on immature turtles.

The paragraphs that follow describe the development of each chapter along with a summary of the main findings. The chapters are ordered by theme, commencing with the global diet of green turtles, then moving onto nesting ecology of green turtles, followed by assessment of population size and growth rates (and effects of satellite tags) of immature turtles.

Chapter Two: Esteban N, Mortimer JA, **Stokes HJ**, Laloë J-O, Unsworth RKF, Hays GC (2020) A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. Mar Biol 167:183. https://doi.org/10.1007/s00227-020-03786-8

For this chapter, I conducted an extensive literature review, collating 177 articles of which 67 of these articles with 89 datasets at 75 sites were included in the review. I extracted diet data from the 89 datasets, categorising diet items into seagrass, macroalgae, terrestrial plants, animal matter and anthropogenic debris and grouped sites into 13 sub-regions in three oceans and one sea. I analysed the diet data to compare the contribution of each major dietary component and compared diet across sub-regions. Although, green turtles were believed to be herbivorous, the key message from this chapter was that green turtle diet varies around the world. We provided the first quantitative evidence that sea surface temperature may be an important driver for green turtle diet as we found predominantly herbivorous diets at warmer sites near the tropics, and more omnivorous diets with higher contributions of animal material at cooler sites. Although other drivers were taken into consideration, we focussed on sea surface temperature as a driver of green turtle diet due to the consistently available global dataset.

Chapter Three: Stokes H J, Esteban N, Hays GC (2023) Nest site selection in sea turtles shows consistencies across the globe in the face of climate change. Anim Behav 208:59-68. https://doi.org/10.1016/j.anbehav.2023.12.001

I was the first scientist permitted to spend an extended period of time on Diego Garcia and stayed eight and four months in 2021 and 2022, respectively. This allowed me to conduct a series of nesting ecology studies to build on previous work by Dr Jeanne Mortimer who started nesting abundance surveys in 1996 with a five-week study (Mortimer and Day 1999). Since then, data collection has been based on track counts conducted bi-weekly by the US Navy Public Works department on Diego Garcia and opportunistically on the outer islands by Fisheries Patrol Officers (Mortimer et al. 2020). My PhD expeditions were planned so I survey during the green turtle nesting season, across the incubation period and increase our understanding of sea turtle nesting ecology in the Chagos Archipelago. During both field expeditions in 2021 (February to September) and 2022 (June to September), I conducted foot patrol surveys to collect data on the position of green turtle nests, distance of the nest from the sea, high water line, and vegetation line and used a theodolite to measure nest height with guidance and assistance in the initial months of each expedition from my primary PhD supervisor, Nicole Esteban. Nests were generally located under vegetation at the back of the beach (90%), where the risk of sea water inundation was low. The remaining 10% were on the open beach in front of the vegetation but were within on average 1.5m of the vegetation. I conducted a review of nest site selection for all species around the world and found that turtles generally crawl a sufficient distance to minimise inundation, although there were slight differences in nest site selection across species and sites depending on beach characteristics.

Chapter Four: Stokes HJ, Laloë J-O, Esteban N, Hays GC. Empirical evidence for the extent of spatial and temporal thermal variation on sea turtle nesting beaches. *Manuscript submitted to J Therm Biol*

My PhD supervisors, Nicole Esteban, and Graeme Hays, along with my co-author Jacques-Olivier Laloë previously monitored and analysed sand temperature between 2012-2014 and found temperatures were relatively cool at Diego Garcia during both hawksbill and green turtle nesting seasons (Esteban et al. 2016). We wanted to expand on these findings using sand temperature data from buried loggers spanning a decade and exploring different sites and habitats across atolls in the Chagos Archipelago to investigate the extent of spatial and temporal thermal variation. In addition to the buried sand temperature logger data, over 10 survey days in 2021 and 2022, I recorded spot sand temperature measurements using a compost probe. I collected data from Diego Garcia, Nelsons Island and Egmont Atoll at different sites along the nesting beach and different nesting habitats (vegetated, a few metres into the vegetation and the open beach). I collected data from Diego Garcia on three consecutive days across different seasons. One objective was to extend the study to other atolls however, unfortunately due to logistics on board the MPA patrol vessel I was unable to visit and conduct probe measurements on further occasions. Supported by Jacques-Olivier Laloë for consistency with previous analysis, I analysed the logger and probe sand temperature data and found the main drivers of thermal variability were seasonal and inter-annual differences modulating sand temperatures by up to 3.00°C and 1.03°C, respectively. Intra-beach and inter-beach variability further modulated temperatures by up to 1.01°C and 0.62°C, respectively. The wide range of temperatures at nesting habitats across the archipelago suggests that both male and female-biased clutches are produced across the nesting seasons.

Chapter Five: Stokes HJ, Esteban N, Hays GC (2023) Predation of sea turtle eggs by rats and crabs. Mar Biol 171:17. https://doi.org/10.1007/s00227-023-04327-9

Over the same period of surveys conducted for Chapter two, I counted eggs laid within a clutch and conducted nest excavations to understand hatching success which also led onto an investigation of the predation of green turtle eggs. During foot patrol surveys for track and nest counts, there were signs of predation from eggshells on the sand surface and near native coconut crab (*Birgus latro*) burrows. I opportunistically observed unmonitored nests where eggs had been removed from recently laid clutches and observed large coconut crab burrows into nests. I found these large burrows presented an opportunity for invasive rats (*Rattus rattus*), and ghost crabs (*Ocypode spp*.) to scavenge eggs from nests. From nest excavations, I calculated the percentage of eaten eggs within and removed from the nest and found 3.1% of eggs were eaten within the nest and 13.9% of eggs were removed. I conducted a literature search to review predators of sea turtle eggs around the world and identified 36 predators, 30 of which were native and eight invasive. Depending on location a predator could be classified as invasive and native. After these observations, I decided to set up surveillance cameras to capture predation rates but unfortunately the cameras did not work as intended. Although, this is an avenue for future research into the correct setup of cameras to monitor predation on Diego Garcia.

Chapter Six: Stokes HJ, Hays GC, Esteban N. Camera trapping: A novel approach to assess population estimates of nesting sea turtles. *Manuscript in preparation*

As previous estimates have been based on track counts from six-week surveys (Mortimer and Day 1999) and two-weekly foot patrol surveys (Mortimer et al. 2020), due to the remoteness of the Chagos Archipelago, camera trapping was trialled as an alternative tool to count tracks on nesting beaches. I setup camera traps along the nesting beaches across three of the five islanded atolls in the Chagos Archipelago. Unfortunately, cameras went missing, assumed stolen, from the outer islands, but I was able to obtain images from the camera traps on Diego Garcia. From these images, I counted tracks, track longevity, and the distance observed from the image to assess how much of the beach was covered by camera traps in one given period. For 91 days we were able to validate extrapolated results from the camera traps with foot patrol surveys as both surveys ran parallel. I calculated track longevity from camera trap images and found tracks lasted on average 3.1±2.2 days around spring tides and 4.1±2.2 days over neap tides, converging with similar findings as Mortimer et al. (2020). We ran a simulation informed by the length and typical number of tracks on Diego Garcia to assess how the extent of beach covered by camera traps influenced the confidence in the estimate of the mean number of tracks per day and found that the extent of sampling variation decreased as camera trap coverage increased. This simulation could be run for different nesting sites with differing length beaches and density of tracks. The findings here highlight how camera traps can be used as a complimentary tool at remote sites to increase temporal coverage and estimate nesting populations.

Chapter Seven: Stokes HJ, Mortimer JA, Laloë J-O, Hays GC, Esteban N (2023) Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. Ecosph 14:e4444. https://doi.org/10.1002/ecs2.4444

My primary PhD supervisor Nicole Esteban conducted trial UAV surveys at Turtle Cove, Diego Garcia in 2018 and 2019. When my field work was delayed for six months, as well as the green turtle global diet review, writing method protocols, and expedition preparation, I undertook initial analysis of the UAV videos. Experiences from the initial trials and video analysis led to a new design for transect flight paths, and an opportunity to mark turtles with white paint prior to UAV surveys to estimate population abundance following procedures outlined in Dunstan et al. (2020). I analysed hours of UAV footage to count turtles and measured straight carapace length and straight carapace width from screenshots to calculate length-to-width ratios and assign species. Green turtles were generally wider, whilst hawksbill turtles were more elongated. From this analysis, I estimated a total of 339 turtles in the lagoon with a density range at different tidal heights between 264 turtles per km^{-2} at high water and 499 turtles km^{-2} at low water. Of these 91% were hawksbills and 9% were green turtles. These density estimates seemed quite high and so I conducted a literature search to collate the density estimates of immature hawkbill turtles at development sites around the world and found out of 17 sites, the hawksbill densities recorded at Turtle Cove were the highest in the world. These findings reflect the long-term protection of turtles in the Chagos Archipelago.

Chapter Eight: Stokes HJ, Stokes KL, Mortimer JA, Laloë J-O, Esteban N, Hays GC. Assessing the impact of satellite tagging on growth rates of immature sea turtles. *Manuscript submitted to Methods Ecol Evol*

During the first field expedition of my PhD in 2021, we conducted mark-recapture surveys at Turtle Cove for a UAV study (chapter six) and it was apparent that many immature turtles were still equipped with satellite tags attached during 2018 and 2019 expeditions. The satellite tags were no longer transmitting and easily removed. A frequently asked question with ethical considerations for tagging animals is how does the device affect the animal? In most cases there is often little to no opportunity to re-capture the individual post tagging and there is no assessment of the effects from tagging. Yet here we had the opportunity to do so. Dr Nicole Esteban and I were able to remove satellite tags during the first survey and I continued to conduct capture-mark-recapture surveys to collect biometric data and remove satellite tags monthly for seven-months to further increase the sample size for growth rates from satellite tagged individuals. I collated data from captures between 2018-2023 and calculated and compared growth rates from 10 tagged and 44 untagged individuals. I analysed the data with input from all co-authors and found that growth rate exponentially decreased as turtle size increased. There was no significant difference in growth rate between tagged and untagged individuals, and no apparent damage to the carapace from tag attachment. Although, the findings from this study were positive we highlighted the need for best practice to study long-term effects of satellite tagging at other sites around the world as foraging range, behaviour, and habitat may influence the potential impact of carrying such devices.

CHAPTER TWO: A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels

Photo credit: RD and BS Kirkby

This chapter was amended from published work:

Esteban N, Mortimer JA, **Stokes HJ**, Laloë J-O, Unsworth RKF, Hays GC (2020) A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels. Mar Biol 167:183. https://doi.org/10.1007/s00227-020-03786-8

Disclaimer: NE, JAM and GCH conceived the study. HJS, JAM and NE conducted the diet literature review, NE carried out the SST global analysis. JOL collated and analysed the SST dataset. NE, JAM and GCH led the writing of the manuscript with contributions from all authors.

ABSTRACT

To better understand dietary requirements, trophic shifts, and trophic interactions of the threatened green turtle (*Chelonia mydas*), we conducted a comprehensive global review and literature tabulation (177 studies) reporting diets of individuals >25 cm carapace length. We analysed those studies involving natural sites and healthy animals that reported relative proportions of all diet components (67 studies, 89 datasets at 75 sites, 13 geographic sub-regions, 3 oceans). We compared diets by sub-region and foraging site relative to four diet components, i.e., seagrass, macroalgae, terrestrial plants (including mangroves) and animal matter. To assess sea surface temperature (SST) as an environmental driver of green turtle diet, values were extracted from satellite data (single year) and site-specific observations (study durations) and examined relative to diet composition. Satellite data indicated that at warmer sites with temperatures >25°C (≥6 months annually), diet was predominantly herbivorous (mean = 92.97%; SE = 9.85; n = 69 datasets). At higher latitude sites and in cold-water currents with SST <20°C (≥6 months annually), dietary animal matter featured prominently (mean = 51.47%; SE = 4.84; n = 20 datasets). Site specific observations indicated that SST had a small but significant effect on contributions of animal matter (r^2 = 0.17, P = <0.001) and seagrass (r^2 = 0.24, P = <0.001) but not macroalgae and terrestrial plants. Our study presents the first quantitative evidence at a global scale that temperature may be an important driver of omnivory, providing a new perspective on variations in green turtle diet, especially in light of global warming and climate change.

KEYWORDS

Cheloniidae, conservation, endangered species, diet composition, herbivore, macroalgae, seagrass meadows, SST, climate change, gelatinous macrozooplankton

INTRODUCTION

Dietary studies are vital to understanding the ecological role of organisms and their trophic interactions (Duffy et al. 2007), which for large marine vertebrates are often not well understood (Matich et al. 2011). Moreover, a better understanding of dietary requirements may help resource managers respond to shifts in trophic interactions between taxa (Brodeur et al. 2017) and, for sea turtles, more effectively prioritize conservation zones and policies for foraging grounds (Hamann et al. 2010; Rees et al. 2016).

Due to numerous anthropogenic threats and population declines, the green turtle (*Chelonia mydas*) was previously listed as globally Endangered on the IUCN Red List (Seminoff 2004). Successful conservation strategies, such as protection of nesting turtles and nesting and foraging habitats, have led to long-term population recovery at many sites (Chaloupka et al. 2008; Mazaris et al. 2017; Silva et al. 2017; Mortimer et al. 2020), resulting in IUCN downlisting of various green turtle subpopulations (e.g., Broderick and Patricio 2019). While sea turtles are particularly vulnerable at their breeding grounds which are easily accessible to humans, they spend most of their lives at their foraging grounds (Hays et al. 2014). Green turtles can migrate vast distances across international borders between breeding and feeding grounds (Hays and Hawkes 2018; Hays et al. 2020) and maintain tight fidelity to their foraging grounds over successive migrations (Shimada et al. 2020). These complex life history strategies highlight the need to improve understanding of green turtle foraging behaviour in different regions and habitats (Klein et al. 2017).

Turtle dietary composition can be assessed by a variety of techniques (Jones and Seminoff 2013). Traditional methods include direct observation using snorkel or SCUBA (Reisser et al. 2013), the analysis of gut contents from dead turtles (Mortimer 1981) and oesophageal lavage and faecal examination (Seminoff et al. 2002), while indirect biochemical approaches include stable isotope analysis (SIA) (Pearson et al. 2017). Modern technologies such as remote videography (Letessier et al. 2014), animal-borne cameras (Heithaus et al. 2002), autonomous underwater vehicles (Dodge et al. 2018) as well as satellite tracking from nesting beach and subsequent *in situ* validation of diet at foraging locations (Esteban et al. 2018) have also been used to document the activities of turtles at their foraging habitats.

The green turtle has been associated with seagrass meadows beginning with early observations in the Indian Ocean (Frazier 1971; Hirth et al. 1973) and long-term studies in the Caribbean (e.g., Bjorndal 1980; Mortimer 1981; Vander Zanden et al. 2013) that reported a herbivorous diet dominated by seagrasses. This seagrass diet is thought to have the wider functional role of supporting seagrass ecosystem resilience (Christianen et al. 2019). Post-hatchling green turtles are believed to spend their first 3-10 years, depending on the ocean basin (Reich et al. 2007; Arthur et al. 2008) in open ocean pelagic habitat and then typically recruit to neritic habitats where their diets tend to shift from omnivorous to primarily herbivorous (see Jones & Seminoff 2013; Howell et al. 2016; Vélez-Rubio et al. 2016; Burgett et al. 2018). Recruitment size (based on curved carapace length (CCL)) varies across populations from 20-25 cm in the western Atlantic (Bjorndal & Bolten 1988) to 30-35 cm in the Indo-Pacific (Limpus et al. 1994) and 30-45 cm in the southwestern Pacific (Arthur et al. 2008) and north central Pacific (Parker et al. 2011).

Seagrasses dominate the diet of green turtles at a range of sites across the Mediterranean (Margaritoulis & Teneketzis 2003; Cardona et al. 2010; Karaa et al. 2012), Indian Ocean (Hasbún et al. 2000; Whiting et al. 2007; Stokes et al. 2019) and Pacific Ocean (Limpus & Reed 1985; Arthur et al. 2009, Prior et al. 2016). At foraging sites where seagrass is absent or sparse, green turtle diet is supplemented or dominated by macroalgae, for example, in Japan (Shimada et al. 2014), Queensland, Australia (Garnett et al. 1985; Prior et al. 2016), Cocos-Keeling Islands (Whiting et al. 2014), Mexico (López-Mendilaharsu et al. 2005), Turkey (Özdilek et al. 2015), Uruguay (Darré Castell et al. 2005), and Galapagos (Páez-Rosas et al. 2021). Terrestrial plant material, especially mangrove leaves and propagules, can also feature prominently in green turtle diets at some sites (Arthur et al. 2009; Nagaoka et al. 2012). Although green turtles are primarily herbivorous, reports of a wide ranging diet of seagrass, marine algae and invertebrates (Jones and Seminoff 2013) include purposely ingested animal matter such as gelatinous macrozooplankton (e.g., scyphozoan jellyfish and salps), sponges, molluscs and fish (Mortimer 1981; Bjorndal 1997; Burkholder et al. 2011; Fukuoka et al. 2019; Piovano et al. 2020).

Studies in the eastern Pacific (Etnoyer et al. 2006), the Mediterranean (Cardona et al. 2010) and in the southwestern Atlantic (Santos et al. 2015) have suggested a relationship between green turtle omnivory levels and sea surface temperature (SST). Nevertheless, regional variations in diet, and the possible role of SST as a driver of these variations have not been examined at a global scale. Here we investigate the diet of green turtles greater than 25 cm CCL (i.e. beyond the presumed 3-10 year-long post-hatchling pelagic stage) in various parts of the world. Specifically, we (1) reviewed literature to assess variation and patterns in the diets of immature and adult green turtles from foraging sites around the globe; (2) analysed the relationship between SST and diet globally to assess SST as a potential driver of omnivory; and (3) examined other possible drivers of green turtle diet that we encountered in the literature. The results of our study will provide a better understanding of diet variation across oceans and help guide green turtle conservation management especially in the context of global warming.

MATERIALS AND METHODS

Global review of green turtle diet

We conducted a literature search in April 2020 for papers of ‘All document types’ and ‘All languages’ on Web of Science using the search term: ALL=(green turtle* OR *Chelonia mydas*) AND ALL=(diet* OR forag*) and Google Scholar using the search term: TOPIC (‘green turtle*’ OR ‘*Chelonia mydas*’) AND (‘diet*’ OR ‘forag*’). Literature citations in the most recent and comprehensive articles located were then checked for studies of green turtle diet; in many cases these involved grey literature that might have been missed by Web of Science or Google Scholar searches. We worked our way back through historical literature in this manner until no more studies reporting diet could be found.

To produce our global review of green turtle diet, we excluded studies of green turtles with carapace length < 25 cm CCL (e.g., Boyle & Limpus 2008) on the assumption that they represented the 3-10-year-old post-hatchling pelagic life stage. We also excluded diet studies if they did not report the relative proportion of all dietary components (e.g. Russell and Balazs 2009) or were from a large-scale pelagic fishery with unknown foraging location (e.g., Parker et al. 2011; Wedemeyer-Strombel et al. 2015). Studies of turtles that were diseased or stranded were excluded due to potential bias in diet as were those of unknown foraging location (e.g., Riosmena-Rodriguez et al. 2011; Souza 2019). We excluded diet studies of captive or artificially fed turtles (e.g., Monzón-Argüello et al. 2018), along with data describing the diets of gravid female green turtles which can differ significantly from those of males, non-breeding females and immature turtles even at shared foraging habitat (Stokes et al. 2019). Where multiple studies from the same site utilised the same dataset, the most detailed study was included (e.g., Arthur et al. 2009; Arthur et al. 2006). Excluded studies were compiled and reasons for their exclusion provided (Appendix Table S2.1).

Where there was no significant difference in diet between multiple sites in one study, data were presented for a centrally located site (e.g., Arthur & Balazs 2008; Stokes et al. 2019). Many of the studies we reviewed did not distinguish size classes, and did not report diet data for immature and adult individuals separately, especially when both occurred together at a benthic foraging site (e.g., Forbes 1996; Read & Limpus 2002; Prior et al. 2016). We therefore pooled our findings on the diet for both immature (> 25 cm CCL) and adult breeding turtles.

In our global review, we recorded the methodologies employed by each study, i.e., gut content analysis, oesophageal lavage, SIA, etc., and tabulated the proportions of individual diet items encountered. We converted results from animal-borne camera studies to diet proportion by dividing the number of bites or feeding events for a diet item (e.g. seagrass) by the total number of bites or feeding events for all diet items. We assigned each type of diet item to one of six categories. The four key nutritional categories were: seagrass, macroalgae, terrestrial plants (e.g., fruits and leaves of mangroves *Avicennia marina*, *A. schaueriana*, *A. germinans*, *Rhizophora mangle* and saltmarsh *Spartina alterniflora*; leaves of *Ficus spp*, *Hibiscus spp*, *Ochroma spp*), and animal matter. The fifth and sixth categories were anthropogenic debris (e.g., plastic fibre) and ‘other’. The category ‘other’ was not always defined in studies but, where defined, included substrate (sand, shell, stone), very digested material, unidentifiable material and natural debris (e.g., bird feathers, wood fragments, etc.). We overlaid green turtle diet composition as defined by the six categories onto a world map shapefile (Made with Natural Earth) using QGIS v3.0, including the available global seagrass distribution (UNEP-WCMC and Short 2018) for reference.

We organized the global diet studies into geographic sub-regions (Appendix Tables S2.1-2.2) based on maps produced by Wallace et al. (2010) to define the global distribution of regional management units (RMUs) of green turtles. An RMU comprises a breeding unit of turtles above the level of the nesting populations but below the level of species within a sub-region, and the RMU maps roughly indicate the distribution of animals belonging to an RMU breeding unit. For our purposes, the geographic boundaries defined by these RMU maps (excluding some areas of overlap) provided objective criteria with which to organize and then compare global studies of turtle diet by sub-region, including all diet data collected for both adults and immature turtles within each sub-region. Our 13 sub-regions corresponded with the following 13 map-defined RMUs (Wallace et al. 2010): Pacific North Central, Pacific East, Atlantic North West, Atlantic South West, Atlantic East, Mediterranean, Indian South West, Indian North West, Indian North East, Indian South East, Pacific South West, Pacific South Central, and Pacific North West. Fig. 2.1a provides a map of the 13 sub-regions and their abbreviations.

Relationship between green turtle diet and SST

We assessed the relationship between green turtle diet and SST at two spatial resolutions. First we used a global scale satellite-sourced SST dataset to present a visual overview. We then used *in situ* surface observations of SST from the International Comprehensible Ocean-Atmosphere Data Set (ICOADS) to obtain higher resolution coastal SST data for each foraging site for fine-scale analysis.

Global SST overview. To produce a visual global overlay map of SST at each of the study sites included in this study, global day-night monthly SST averages, during a single year, derived from the AVHRR Pathfinder (Version 5, 4 km) SST cloud screened data set (Phillips et al. 2012) were downloaded and projected on ArcMap version 10.5.1. Although accuracy and precision of satellite sourced SST at the coastline is lower than SST measurements made *in situ* (Brewin et al. 2018), this data set was used for the global overview as it provides the longest, accurate and highest resolution SST climate data record for analysis of global SST (NCAR 2014). The data set was not available for the entire time series. We selected the year 1993 for two reasons: it represents the midpoint of the sampling period for the diet studies (1971-2016); and it lacked El Niño and La Niña events (NOAA 2020). Quarterly periods (Jan-Mar, Apr-Jun, Jul-Sep, Oct-Dec) were selected to represent seasonal variation in temperature at different sites.

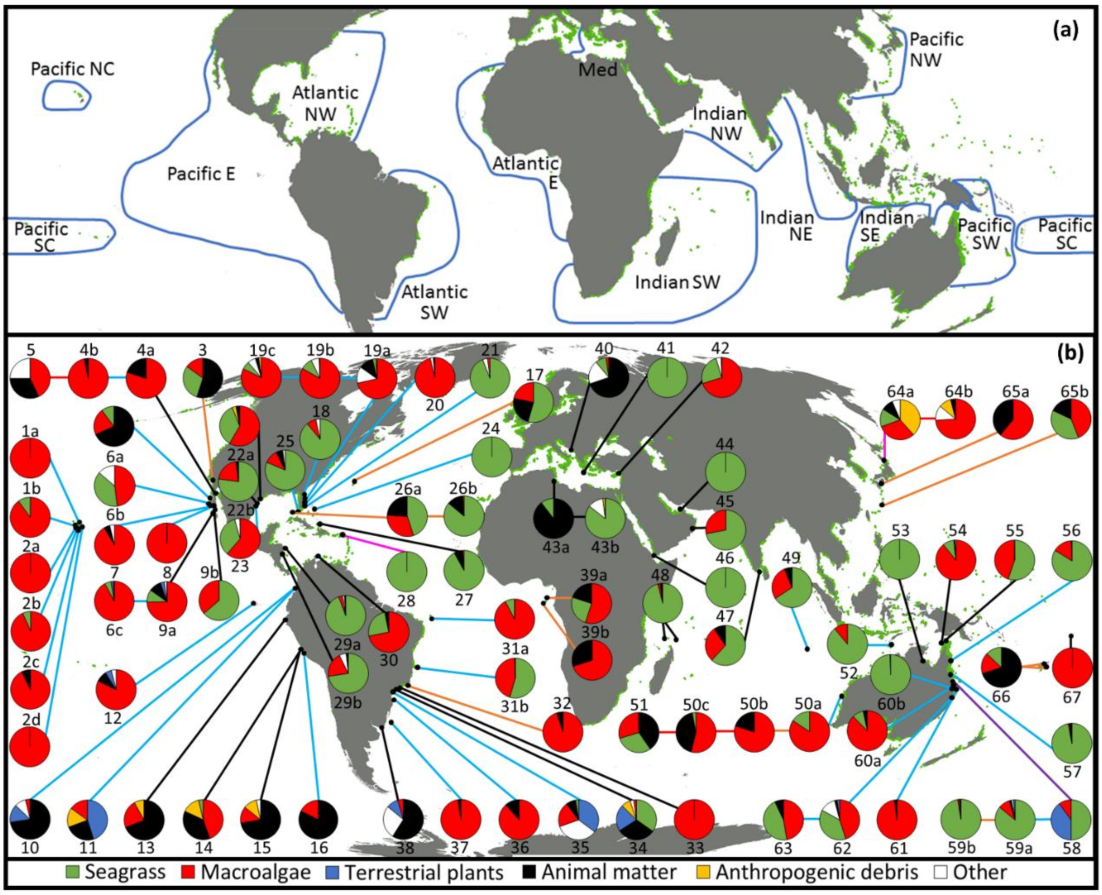

Figure 2.1. Comparison of green turtle diet composition across the globe. (a) 13 geographic sub-regions, based on maps of the *Chelonia mydas* RMUs (adapted from Wallace et al. 2010), were used to compare diet composition. Moving from west to east these include: Pacific North Central (Pacific NC), Pacific East (Pacific E), Atlantic North West (Atlantic NW), Atlantic South West (Atlantic SW), Atlantic East (Atlantic E), Mediterranean (Med), Indian South West (Indian SW), Indian North West (Indian NW), Indian North East (Indian NE), Indian South East (Indian SE), Pacific South West (Pacific SW), Pacific North West (Pacific NW), Pacific South Central (Pacific SC). (b) The proportion of contribution made by each of six categories of diet items recorded in 89 datasets at 75 sites are shown by segments of the pie charts. The term 'Other' is not always defined and includes substrate, very digested material, and natural debris (e.g., feathers). Methods used to study diet are represented by coloured lines—i.e., gut content analysis (black), oesophageal lavage (blue), SIA (orange), mouth content (purple), faecal examination (pink) and animal-borne camera (red) studies. Green dots indicate known seagrass observation data points (Source: UNEP-WCMC and Short,

2018, see Appendix Fig. S2.1-A2.4 for fine scale maps). Numbers indicate source literature (see Appendix Table S2.1 for study site, analytical method, diet group and results), and break-down by sub-region as follows: Pacific NC (1-2), Pacific E (3-16), Atlantic NW (17-30), Atlantic SW (31-38), Atlantic E (39), Med (40-43), Indian NW (44-47), Indian SW (48), Indian NE (49), Indian SE (50-52), Pacific SW (53-63), Pacific NW (64-65), and Pacific SC (66-67).

Foraging site SST. We extracted *in situ* observations of SST data for the 1° by 1° pixel around each foraging site from ICOADS (NCAR 2015). We obtained data from the Enhanced ICOADS Monthly Summary Release 3.0 at the 1-degree spatial resolution for the 12 months, from January to December, that coincided with the sampling period of each respective study, e.g., if sampling took place in 2005 and 2006, then SST data were included from January 2005 through December 2006. There are fewer sites included in the analysis of SST at foraging sites than in the global SST overview. This is because we avoided potential bias due to under-sampling by excluding those seven datasets with < 10 SST observations per month. Some of these datasets were for the same site and three sites were excluded from further analysis because SST data were unavailable, i.e., South Caribbean Nicaragua, Torres Strait Australia, and Tokelau. Multiple diet composition datasets existed across several sampling periods at some sites, e.g., Bahia de los Angeles, Mexico and Shark Bay, Australia and are included in the analysis. We calculated the mean annual SST, the maximum annual SST and the minimum annual SST for each site.

Data analysis

The average contribution of each of the six major dietary components of green turtle diet (seagrass, macroalgae, terrestrial plants, animal matter, other, and anthropogenic debris) were compared using a Kruskal-Wallis rank sum test. To compare diet across sub-regions, a Dunn's (1964) test was used to calculate multiple comparison p-values adjusted with the Benjamini and Hochberg (1995) method. For the foraging site SST analysis, dietary component data were arcsine-square-root transformed. Linear regression was used to explore the relationship between diet content data and SST at foraging sites. Figures are presented showing untransformed (Figs. 2.1-2.3) or back transformed data (Fig. 2.4; Appendix Fig. S2.5) for ease of interpretation. Statistical analyses were performed using R (R Core Team 2017). Mean ± SE values are presented unless otherwise indicated. The significance level of all statistical tests was set at $\alpha < 0.05$.

RESULTS

Global review of green turtle diet

Of the 177 articles examined, 67 articles with 89 datasets describing diet composition of green turtles at 75 sites around the world met the criteria for inclusion in our review (Fig. 2.1; Appendix Table S2.1). An additional 110 diet studies were excluded from further analysis for the following reasons: unspecified diet composition (n = 40) or foraging location (n = 7); sampling of stranded dead/diseased individuals (n = 28), captive turtles with artificially fed diet (n = 11), or nesting females (n = 3); focus on ingestion of anthropogenic debris (n = 17); turtles below minimum carapace size (n = 2); or duplicate dataset (n = 2). See Appendix Table A2.2 for study details and exclusion reasons.

The datasets in studies that met our criteria spanned 13 sub-regions in three oceans and one sea: Pacific N Central (Hawaii) (n = 6), Pacific E (off North, Central and South America) (n = 18), Atlantic NW (off North and Central America, including Caribbean) (n = 19), Atlantic SW (off South America) (n = 9), Atlantic E (São Tomé Island) (n = 2), Mediterranean (n = 5), Indian NW (Arabian Peninsula and India) (n = 4), Indian SW (Seychelles) (n = 1), Indian NE (Cocos-Keeling) (n = 1), Indian SE (Western Australia) (n = 5), Pacific SW (Eastern Australia) (n = 13), Pacific NW (Japan) (n = 4) and Pacific S Central (Fiji and Tokelau) (n = 2). The relative prominence of the following four key nutritional categories were reported across sites and are considered in our analysis: seagrass, macroalgae, terrestrial plants, and animal matter. The amount of anthropogenic debris in the diet also varies between sites. Nevertheless, some patterns emerge (Figs. 2.1 and 2.2). An expanded version of Fig. 2.1 (Appendix 1 Figs.

S2.1-2.4) shows details of regional seagrass distribution as well as contribution of the six categories of diet items.

Seagrass dominant. Seagrass contribution to diet is greatest in the following sub-regions: Indian SW (mean = 95.0%; n = 1; Stokes et al. 2019), Indian NW (mean = 83.3%; SE = 9.6; n = 4; e.g., Hasbun et al. 2000), Indian NE (mean = 65.1%; n = 1; Whiting et al. 2014), Pacific SW (mean = 59.3%; SE = 10.4; n = 13; e.g., Fuentes et al. 2006; Prior et al. 2016), Atlantic NW (mean = 57.5%; SE = 8.2; n = 19; e.g., Mortimer 1981; Stringell et al. 2016) and Mediterranean (mean = 46.0%; SE = 19.4; n = 5; e.g., Karaa et al. 2012). All studies that recorded no seagrass (or virtually none) in the diet are from regions with limited documented seagrass distribution (e.g., Pacific E and Atlantic SW) (Fig. 2.1; Appendix Figs. S2.1-S2.4).

Macroalgae dominant. Macroalgae is consumed most abundantly in the following sub-regions: Pacific N Central (mean = 96.0%; SE = 1.9; n = 6; e.g., Arthur & Balazs 2008; Balazs et al. 1987), Atlantic E (mean = 62.5; SE = 7.5; n = 2; e.g., Hancock et al. 2018), Atlantic SW (mean = 59.5%; SE = 13.9; n = 9) especially tropical areas (e.g., Reisser et al. 2013), Pacific S Central (mean = 58.5; SE = 41.5; n = 2; e.g., Piovano et al. 2020; Balazs 1983), Pacific NW (mean = 52.5%; SE = 9.4; n = 4), Indian SE (mean = 51.7%; SE = 14.2; n = 5; e.g., Shimada et al. 2014; Fukuoka et al. 2016), Pacific E (mean = 49.4%; SE = 7.7; n = 18; e.g. Seminoff et al. 2002; Arthur & Balazs 2008; Carrión Cortez et al. 2010; Quiñones et al. 2010), and Atlantic NW (mean = 34.1%, SE = 7.7; n = 19) especially high in temperate areas (e.g., Holloway-Adkins & Hansiak 2017).

Seagrass and Macroalgae. Nearly equal proportions of both seagrass and macroalgae have been recorded in diets in the following sub-regions: Pacific E (López-Mendilaharsu et al. 2005), Atlantic NE in the Gulf of Mexico (Howell et al. 2016), Indian SE at Cocos (Keeling) islands (Whiting et al. 2014), and Pacific SW at Torres Strait (Andre et al. 2005).

Terrestrial plants. Terrestrial plant contribution is highest in the following sub-regions: Atlantic SW (mean = 8.3%; SE = 4.7; n = 9) especially at estuarine sites, e.g., from 10% in Argentina (González Carman et al. 2014) to 35% in Brazil (Nagaoka et al. 2012); Pacific E (mean = 3.7%; SE = 2.3; n = 18) especially at estuarine sites (e.g., 38% in Colombia, Sampson et al. 2018), and where mangrove fruits and leaves featured (e.g., 5% in the Galapagos Islands, Carrión-Cortez et al. 2010; 3.2% in Mexico, López-

Mendilaharsu et al. 2005); and Pacific SW (mean = 3.5%; SE = 3.0; n = 13) where mangrove cotyledons, leaves and fruit formed 40% of the diet in Shoalwater Bay, Queensland Australia (Limpus & Limpus 2000).

Animal matter. Animal matter featured to some degree in all sub-regions, especially the following: Pacific S Central pelagic sites (mean = 35%; SE = 35; n = 2; e.g., Piovano et al. 2020); Pacific E neritic sites (mean = 30.9%; SE = 7.2; n = 18; e.g., Amorocho & Reina 2007; Jiménez et al. 2017; Quiñones et al. 2010; Paredes 2015); Mediterranean neritic sites (mean = 31.9%; SE = 19.7; n = 5; e.g., Lazar et al. 2010; Karaa et al. 2012); Indian SE neritic sites (mean = 20.7%; SE = 9.3; n = 5; e.g., Burkholder et al. 2011; Thomson et al. 2018); and at Atlantic E upwelling sites (mean = 25%; SE = 5; n = 2; e.g., Hancock et al. 2018).

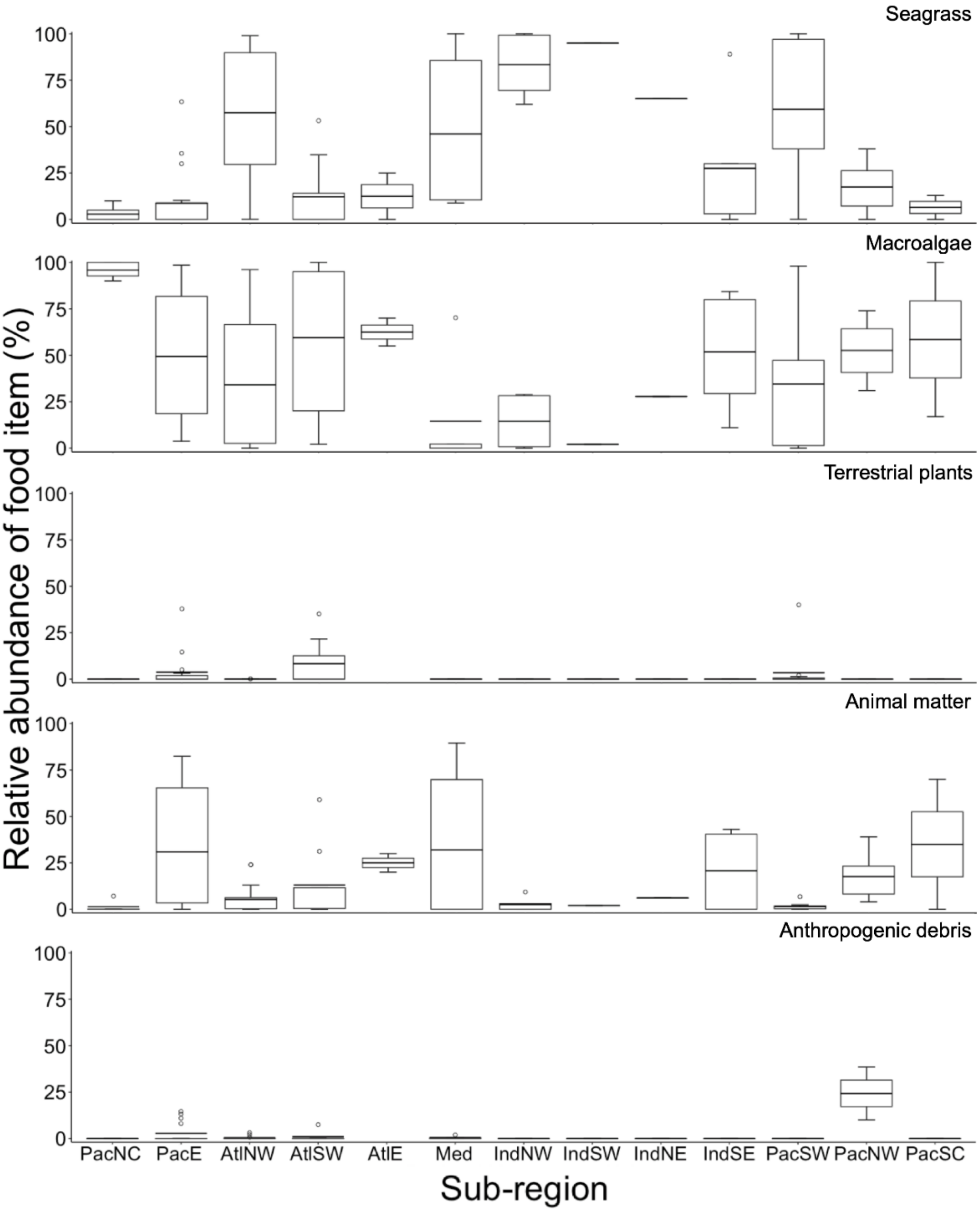

Figure 2.2. Comparison of the relative abundance of food items in green turtle diet across the globe: seagrass, macroalgae, terrestrial plants, animal matter and anthropogenic debris. The diet item percentages were collated from 89 datasets at 75 sites across 13 sub-regions for sea turtles (see Appendix Table S2.1 for study site, analytical method, diet group results, source literature). Bold horizontal lines indicate mean, boxes delineate the upper and lower quartiles and whiskers define the data's range. Outliers are plotted as separate points. A comparison of the proportion of seagrass consumed by green turtles between sub-regions showed significant and

major differences (Kruskal-Wallis test, $H_{12} = 45.17$, $p < 0.001$). Multiple comparisons showed a significant difference between green turtle diet recorded in the Atlantic NW and Atlantic SW ($p = 0.02$), Atlantic SW and Indian NW ($p = 0.03$), Atlantic NW and Pacific E ($p = 0.002$), Indian NW and Pacific E ($p = 0.008$), Atlantic NW and Pacific N Central ($p = 0.01$), Indian NW and Pacific N Central ($p = 0.01$), Atlantic SW and Pacific SW ($p = 0.02$), Pacific E and Pacific SW ($p = 0.002$), Pacific N Central and Pacific SW ($p = 0.01$). The amount of anthropogenic materials present varied amongst sites but was most abundant in the Pacific Ocean (Pacific E and Pacific NW) (Fig. 2.1; Fig. 2.2; Appendix Table S2.1).

Relationship between green turtle diet and SST

Global SST overview. A global comparison of principal diet components (plant-dominated diet vs omnivorous diet) with seasonal SST provides an indication of the relative importance of SST on diet at different sites (Fig. 2.3). Our findings suggest that at cooler sites where SST is < 20°C for ≥ 6 months each year, animal matter in the diet is always > 20% (range = 20.3-89.5%; mean = 51.48 ± 4.84%; n = 14 sites; n = 20 datasets). These areas are at higher latitudes (e.g., California USA, Argentina and Croatia), close to cold water currents or upwellings (e.g., Colombia and Peru) or in areas of overlapping climate zones (e.g., Brazil). Generally, at warmer sites where SST ≥ 25°C for 9-12 months, green turtle diet is almost always ≤ 20% animal matter and is dominated by plant matter (mean = 92.97 ± 1.19%; range = 45.5-100%; n = 57 sites; n = 69 datasets).

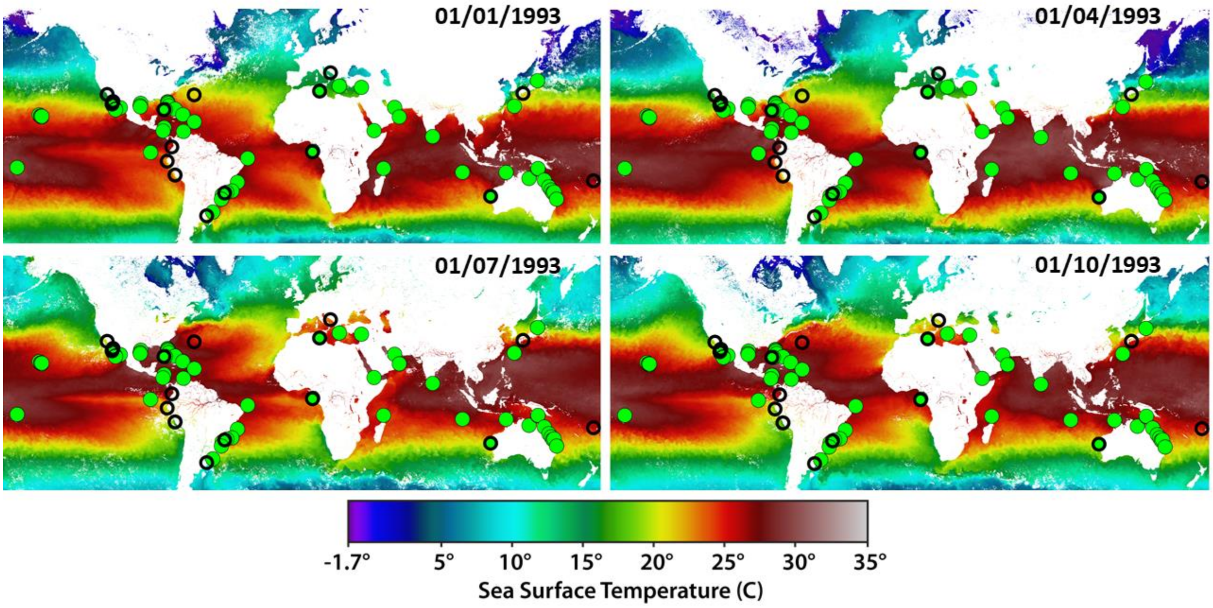

Figure 2.3. The importance of plant or animal content in green turtle diet is related to sea surface temperature (SST). Generally, at higher latitudes and in cold-water currents where SST is < 20°C for at least two seasons, animal matter in the diet is > 20% (black circles; mean = 51.47%; SE = 4.84; n = 14 sites); whereas at warmer sites where SST > 25°C for at least two seasons, green turtle diet is dominated by seagrass, macroalgae and mangroves (green circles; mean = 92.97%; SE = 9.85; n = 57 sites). Both plant and animal matter are important components at a small number of sites (green circles outlined by black, n = 4 sites). SST temperatures from the year 1993 are at the midpoint of the study time series (1971 – 2016; Table S2.1). SST (AVHRR) data source: Phillips et al. 2012.

A few sites around the world are exceptions to the trend of decreasing animal matter with increasing SST. Contradicting diet preference (see Appendix Table S2.1) existed at four sites, each in a different sub-region (Atlantic NW, Atlantic E, Mediterranean and Indian SE). These four sites (i.e., Dry Tortugas Florida USA, São Tomé Island, Gulf of Gabes Tunisia, and Shark Bay Western Australia) are represented by green circles with a black outline (the green circle indicates a plant dominated diet and black outline indicates > 20% animal matter) (Fig. 2.3). Among sites with high SST and expected plant-dominated diet, one notable exception, indicated by a black ring, is Fiji (Pacific S Central) where diet is dominated by 71% animal matter (Piovano et al. 2020). Two exceptions to an expected omnivorous diet at sites with low SST values are the Sanriku coast of Japan (Pacific NW) and Galapagos Ecuador (Pacific E), both indicated by green circles (Fig. 2.3).

Foraging site SST. Analysis of fine-scale SST data from 72 foraging sites shows a similar pattern to that provided by the global SST overview, with a small but significant ($P = < 0.001$) relationship between SST and the proportion of animal matter in the diet (n = 82 datasets). The contribution of animal matter in the diet tended to increase at cooler temperatures (Fig. 2.4; Appendix Fig. S2.5) and the resulting relationship between the percent animal matter and maximum SST was small but significant ($r^2 = 0.16$, $t = -3.7$, $F_{1,72} = 13.32$, $P = < 0.001$). Conversely, the contribution of seagrass to the diet tended to increase with warmer temperatures (Appendix Fig. S2.5). Maximum sea surface temperatures had a small but significant relationship to percent seagrass in the diet ($r^2 = 0.22$, $t = 4.5$, $F_{1,72} = 20.6$, $P = < 0.001$). We also found a small effect of mean SST on percent animal matter and seagrass in the diet, and a small effect of minimum SST on percent seagrass in the diet ($P < 0.05$ in all cases; see Appendix Fig. S2.5). There was no effect of SST on contribution of either macroalgae or terrestrial plants (notably mangrove) to the diet (Appendix Fig. S2.5).

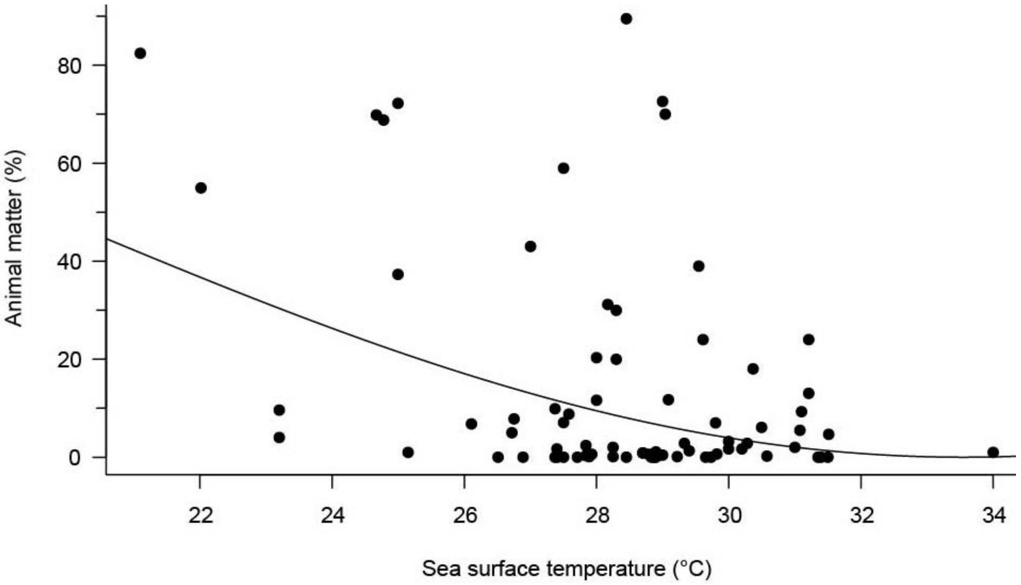

Figure 2.4. Sea surface temperature has a small effect on green turtle diet at foraging grounds: a lower proportion of animal matter is present in the diet of turtles at sites with higher sea surface temperatures (r^2 = 0.16, t = -3.7, $F_{1,72}$ = 13.32, P = < 0.001). Sea surface temperature is shown as maximum annual temperature recorded during the sampling year(s) of 82 datasets from 72 sites in the Atlantic, Indian and Pacific Oceans and Mediterranean Sea. SST (ICOADS) data source: NCAR 2015.

DISCUSSION

Considerable variability in green turtle diet exists around the world, across oceans and within foraging grounds. Our review has captured much of the literature to tease apart spatial variation in green turtle diet and our analysis shows SST to be a driver of omnivory. At most foraging sites included in this study, as expected, green turtles were primarily herbivorous with three categories of plant material featuring in the diet: seagrass predominating at sites where it was abundant; macroalgae where seagrass is relatively sparse or absent; and terrestrial plant material (especially mangrove leaves and propagules, but also other terrestrial species) particularly in estuarine areas. Omnivory also featured at some sites.

Green turtle feeding strategies range from nearly total herbivory at some neritic sites (Stokes et al. 2019) to oceanic omnivory (Turner Tomaszewicz et al. 2018), and at some sites a high degree of omnivory even after settling at neritic habitats through adulthood (Vélez-Rubio et al. 2016). Some green turtles may shuttle between neritic and oceanic environments, as in Fiji (Piovano 2020). This is in contrast to the previously documented and often assumed one-way ontogenetic habitat transition (di Beneditto et al. 2017). Drivers of green turtle diet discussed in the literature include SST, characteristics of the gut biome, prey availability, size classes of turtles and impacts of anthropogenic activities.

SST as a driver of variation in green turtle diet

Our global overview and foraging site-specific analyses showed a relationship between warmer temperatures and a seagrass diet, and lower temperatures and a diet comprising large amounts of animal matter, especially macrozooplankton. We conclude that green turtle omnivory may be partly driven by water temperature, and we present the first quantitative evidence that temperature may be an important driver of diet in green turtles at a global scale, especially where the diet includes gelatinous macrozooplankton (in particular, jellyfish and salps). Gelatinous macrozooplankton featured most prominently at oceanic and extreme-latitude sites in the Pacific and Atlantic, ranging from 40% in the Pacific NW (Fukuoka et al. 2016); 30-73% in the oceanic Pacific NC (Parker et al. 2011; Wedemeyer-Strombel et al. 2015); 38-72% along the Pacific E coastline (Seminoff et al. 2006; Amorocho & Reina 2007; Quiñones et al. 2010; Lemons et al. 2011; Jiménez et al. 2017); and 40-59% in the Atlantic SW (Bugoni et al. 2003; González Carman et al. 2014). A feature shared by all these sites appears to be much cooler water temperatures (< 20 °C) during all or part of the year. Previous studies (e.g., Etnoyer et al. 2006; Cardona et al. 2010; Santos et al. 2015) have shown that green turtle omnivory levels are influenced by SST, but ours is the first study to quantify this relationship on a global scale and highlight differences in green turtle diets in different regions.

Two patterns of geographic distribution of a gelatinous macrozooplankton diet associated with cooler water temperatures are apparent. One appears to correlate with higher latitudes and cooler temperatures (e.g., Pacific E, Pacific SC, Pacific NW, southern Atlantic SW, northern Atlantic NW, and Shark Bay Australia in Indian SE). The second may be mediated by global patterns of the major warm and cold oceanic currents. Warm ocean currents tend to flow away from the equatorial region on the western side of ocean basins, and cold ocean currents flow towards the equator on the eastern side of ocean basins. It follows that cool currents may account for the patterns of high macrozooplankton consumption that appear to be associated with the California Current (off California and Baja California), the Peru Current (off Ecuador, Peru and Columbia), and the Benguela Current (off Mauritania). Water temperature is known to affect the abundance and distribution of food resources in the oceans (O'Connor et al. 2007). At cooler sites, where estimated levels of carnivory are typically > 20%, there is high contribution of gelatinous macro-zooplankton. While latitudinal patterns of gelatinous plankton abundance are not well known, there is some evidence that their abundance may increase at higher latitudes. For example, the leatherback turtle (*Dermochelys coriacea*), which feeds almost exclusively on gelatinous plankton, breeds on tropical beaches but often migrates to forage at high latitudes (e.g. Fossette et al. 2014). A recent review of taxa feeding on gelatinous plankton, showed many examples of pelagic predators from higher latitudes (Hays et al. 2018), including coho salmon (*Oncorhynchus kisutch*), larval/juvenile sablefish (*Anoplopoma fimbria*) and Cassin's Auklet (*Ptychoramphus aleuticus*) in waters off Vancouver Island in the northern Pacific E (Mackas et al. 2007). While there was a significant relationship between SST and the percent of animal matter in the diet, there was still considerable variability in this relationship, suggesting that other factors, in addition to SST, likely also drive the diet at individual sites. Given that we found relatively few diet studies at sites with cooler temperatures (10 – 20 °C, e.g., Brazil), the role of SST may become clearer once more diet studies are conducted at such cooler sites.

Besides gelatinous plankton, there are other animal-based sources of diet that can be grazed from the benthos. For example, neritic habitats in Fiji (Pacific SC) support a green turtle diet dominated by herbivorous (e.g., sea urchin *Tripneustes gratilla*) and carnivorous (e.g., cone shell *Conus ebreus*) invertebrates as well as fish (Piovano et al. 2020). Larger turtles of post-recruitment size and sizes typical of the benthic habitat have been observed in oceanic habitats (Turner Tomaszewicz et al.

2018); and it is possible that turtles employ shifts in foraging behaviour during multiple transitions between the neritic and oceanic habitats of Fiji (Piovano et al. 2020).

Because we used SST data at a relatively course spatial scale, our study would not have identified variations or anomalies in water temperature at the level of the relatively small home ranges that foraging green turtles typically occupy (Christiansen et al. 2017). Likewise, the relationship between green turtle diet and mean SST value derived from the multi-decadal study period is unlikely to capture changes in SST values throughout that time period, nor shifts in green turtle diets on the scale reported by Bell et al. (2019). SST data at a finer spatial and temporal scale, particularly from the shallow nearshore habitats where green turtles typically forage, might shed further light on the role of SST in driving diet.

At some foraging sites temperature does not always predict diet composition. In Japan, low SST values would predict an omnivorous diet, as it does at Shikoku, Japan, where 39% animal matter is reported in the diet (Shimada et al. 2014). But, at an even higher latitude with cooler temperatures on the Sanriku Coast of Japan, the diet comprised only 4-9.6% animal matter in similarly sized turtles (Fukuoka et al. 2016).

Although not the focus of our review, many other environmental effects and limits influence the distribution of food species, such as water depth, substrate type, water clarity, and abundance of other predators that feed on prey consumed by green turtles. Temperature is not always a good predictor of diet, but other variables such as oceanographic features (Cox et al. 2018) and availability of food items could be (e.g., Goldbogen et al. 2015). Improving our understanding of how food availability at foraging sites drives foraging behaviour remains a critical question (Hays et al. 2016).

Some other drivers of variation in green turtle diet

Our review suggests that, in addition to SST, other drivers may influence green turtle diet across and within regions. These drivers may include a combination of factors such as gut microflora, the influence of habitat on spatial and seasonal prey availability, and the size class of turtles. Moreover, there may be synergism between drivers.

Gut microflora

The relationship between water temperature and diet composition may be driven to some extent by physiological factors. If the gut microflora that enables turtles to digest plant material does not function efficiently at lower temperatures, turtles may opt to feed on relatively more animal material (Amorocho and Reina 2007). In the literature, spatial variation in green turtle diet has often been explained by a combination of environment (e.g., food availability, different habitats) and characteristics of the gastrointestinal microbiome which are influenced by diet (Bjorndal 1997; Price et al. 2017). For example, seagrass *Thalassia testudinum* dominates the Caribbean benthos and is the dominant food item (e.g., Stringell et al. 2016); while in the Galapagos (Carrión-Cortez et al. 2010) and at Heron Reef Australia (Forbes 1996) the dominant primary producer is macroalgae which comprises most of the diet. Recent advances in knowledge indicate however, that regardless of diet, the microbiome in green turtles contains the same bacterial phyla although bacterial community composition changes over time in response to diet (Ahasan et al. 2017; Campos et al. 2018; Bloodgood et al. 2020).

At Shark Bay, Australia, even though seagrass habitat dominates, green turtles primarily assimilate energy from macroalgae and gelatinous macrozooplankton. Various hypotheses were proposed by Burkholder et al. (2011) to explain this anomaly including: that macroalgae and gelatinous macroplankton are more digestible than the dominant *Amphibolis antarctica* seagrass; that an individual's diet depends on its intestinal microflora causing a preference for either seagrass or algal dominated diets; or that a high risk of predation by sharks interferes with feeding behaviour. Certainly, Shark Bay appears to be an unusual site where green turtles are highly omnivorous and individuals specialise on varying combinations of seagrasses, macroalgae and invertebrates (Thomson et al. 2018).

Prey availability

We expect food availability will ultimately influence diet composition, with sea temperature providing a proximal influence on diet through its role on prey availability. Foraging strategy (commonly described by the Optimal Foraging Theory) predicts that individuals adjust their movements according to the spatial distribution of their prey so that a more productive environment should lead to more specialised diet (MacArthur & Pianka 1966). In this way, diet composition variation and distribution has been linked to availability of food (or prey) across marine taxa, including seabirds, marine mammals and reptiles (e.g., León & Bjorndal 2002; Pinaud et al. 2005; Hays et al. 2006; Womble and Sigler 2006).

A recent review of intraspecific variation in trophic ecology of sea turtles using SIA confirms the versatility in trophic ecology that has been suggested for green turtles (Figgener et al. 2019), emphasising the cryptic and contrasting nature of diets in adult green turtle populations. Variations in upwelling processes in the Galapagos Islands (Pacific E), affect algal composition leading to higher diversity of red algae in diet at some sites (Carrión-Cortez et al. 2010). In Hawaii (Pacific N Central), differences in the relative availability of seagrass and macroalgae are apparent over short distances. For example, green turtles consumed both seagrass and macroalgae at Kāne’ohe Bay, O’ahu but only macroalgae at other sites amongst the six main islands of Hawaii (Arthur and Balazs 2008). At São Tomé island (Atlantic E), at two foraging sites (separated by 50 km), diet composition indicated distinct isotopic niches: a diet dominated by macroalgae and animal matter at one rocky reef site (with no seagrass) and a mixed diet of seagrass, macroalgae and animal matter at a site with seagrass (Hancock et al. 2018). Besides availability of diet components, it is also important to consider their energy value via nutritional composition (e.g., protein, fat content, Neutral Detergent Fibre (NDF) that affects digestibility). Nutrition analysis for diet of green turtles has been conducted at a number of sites (e.g., Bjorndal 1979; Sampson et al. 2018) and while nutritional composition is known for some prey (e.g., tunicates, algae, seagrass; Amorocho and Reina 2007; Bjorndal 1979) nutritional values are not available for many dietary species (e.g., *Thalassodendron ciliatum* Trevathan-Tackett et al. 2017), and this is an important area for future research.

We were unable to properly analyse the relationship between food availability and diet composition due to lack of detailed data about both sets of variables in individual studies. Nevertheless, all studies that recorded no seagrass in the diet, such as those in the Atlantic SW (Reisser et al. 2013; Darré Castell et al. 2005) and in the southern Pacific E (Carrión-Cortez et al. 2010; Jiménez et al. 2017) were from regions characterised by sparse to non-existent seagrass habitats (UNEP-WCMC & Short 2018). The global distribution layer for seagrass based on point data (UNEP-WCMC & Short 2018) is currently the most accurate dataset available, and although a recent study has estimated seagrass extent worldwide, the authors describe numerous weaknesses in the data (McKenzie et al. 2020) limiting its utility as a quantitative data source. This means the dataset offers no metrics with which to estimate seagrass availability as a driver of amount of seagrass in green turtle diet at a local level.

Size class of turtles

Size class may be expected to play a role in determining rates of omnivory. Studies across taxa demonstrate that individuals maximise growth rates from juvenile to maturity by selecting a high protein diet. This has been demonstrated for a variety of reptiles (e.g., Durtsche 2004; Bouchard & Bjorndal 2006; Wotherspoon & Burgin 2016), which may explain why animal matter is so important for post-hatching green turtles < 25 cm CCL (Hancock et al. 2018). Though, the amount of animal matter consumed by post-hatchings could also be down to prey availability in the open ocean (Boyle and Limpus 2008).

The timing and the size class at which the dietary shift between late pelagic stage and neritic recruitment varies across sub-regions. For example, green turtles in the Atlantic (Bjorndal & Bolten 1988) shift to a neritic life stage at a smaller size than those in the Indo-Pacific (Limpus et al. 1994). Stable isotope studies that sample inert tissues (e.g. bone growth layers) enable assessment of feeding history and determination of the timing of ontogenetic shift, e.g., at 20-25 cm CCL in the Atlantic SW (Bjorndal et al. 2000). This method has been used to show that timing varies across sub-regions in Atlantic SW, Pacific SW, and Mediterranean (see Reich et al. 2007; Arthur et al 2008; Cardona et al. 2010; Gonzalez et al. 2012; Howell et al. 2016). In Uruguay (Atlantic SW), turtles shift from omnivory (gelatinous microzooplankton) to herbivory at approximately 45 cm CCL (Velez-Rubio et al. 2016), but along the NW coast of Africa (Atlantic E) at about 59 cm CCL (Cardona et al. 2009). No clear ontogenetic dietary shift was reported at foraging sites in either the western Pacific, Pacific E, or Atlantic E as levels of omnivory were similar for both juveniles > 25 cm CCL and adults (Lemons et al. 2011; Shimada et al. 2014; Hancock et al. 2018). Nevertheless, intra-population variation in diet composition also exists (Burgett et al. 2018).

Animal matter decreased in importance for larger size classes in the Gulf of Gabes (Mediterranean) (Karaa et al. 2012) and in the Dry Tortugas National Park, Florida (Atlantic NW) (Roche, 2016). At a few sites, larger size classes foraging in tropical seagrass meadows may exhibit high levels of omnivory. For example, at Fiji (Pacific SC) the diet of turtles measuring 43-89 cm CCL was 71% animal matter (40% invertebrates and 31% fishes) (Piovano et al. 2020).

Unfortunately, because many diet studies included in this review did not differentiate between size classes, we were unable to further explore size class as a driver of omnivory. We encourage future diet studies to incorporate size class into their analyses, as it may help clarify timing of the ontogenetic shift from pelagic to neritic habitat.

Anthropogenic impacts

Our review found that the highest levels of anthropogenic debris in the diets of green turtles were in the Pacific Ocean. In the Pacific E, at Sechura Bay, Peru (Jiménez et al. 2017) and in Gorgona Park, Colombia (Sampson et al. 2018), 8% and 13.1% of diet, respectively, comprised anthropogenic debris. In the Pacific NW, green turtles foraging along the Sanriku coast of Japan ingested a range of artificial debris, including hard and soft plastics, styrofoam, fishing line/rope and rubber (Fukuoka et al. 2016). Coastal habitat degradation associated with anthropogenic development, such as that at highly urbanised sites along the east coast of Brazil in the Atlantic SW, affects the diversity of food items and can contribute to low dietary diversity in green turtles (Santos et al. 2011). Furthermore, Santos et al. (2015) report high foraging plasticity amongst green turtles in estuaries that combine an estuarine diet with pelagic foraging, perhaps in response to habitat degradation.

Relative merits and constraints of diet analysis techniques

Our review describes diet composition based on studies that used a variety of analytical methods, each characterised by benefits and disadvantages. Besides less-invasive direct observation of foraging behaviour (e.g., Schofield et al. 2006), two relatively simple and low-cost traditional quantitative methods of gut content analysis provide specific information on the composition, occurrence and quantity of species consumed (Miller et al. 2010). The analysis of a dissected gut provides an unbiased record (Gama et al. 2016) of recently ingested food from the oesophagus (e.g., Stokes et al. 2019). Oesophageal lavage from live animals is more common but only provides an indicative record of food consumed due to relatively small sample sizes produced and selective retention of larger items by oesophageal papillae (Reisser et al. 2013). SIA has developed in the past two decades as a powerful tool to complement these traditional methods of studying diet and trophic ecology (see review by Haywood et al. 2019). Analysis of the composition of stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) in tissues with different residence times provides historical evidence of diet and patterns of ontogenetic shift (Arthur et al. 2008; Cardona et al. 2009; Vander Zanden et al. 2013; Vélez-Rubio et al. 2018). For example, blood serum represents food consumed recently and epidermal tissue or scutes represent the diet consumed several months previously (Reich et al. 2008). In some cases, however, SIA may over-estimate the relative volume of animal matter in the diet because a higher proportion of animal-sourced $\delta^{15}N$ may be assimilated into the tissues compared with plant-sourced $\delta^{15}N$; or it may misrepresent relative contributions of different types of plant matter (Lemons et al. 2011; Bezerra et al. 2015). Remote videography can provide insights to diet composition however it is difficult to calculate the relative contribution to diet from video observations of bite counts without support from other techniques (Thomson et al. 2018).

The results of diet studies can be biased by the type of sampling used. Broadly, gut contents represent ingestion and SIA values measure assimilation. Bite counts/events from video footage may not provide an accurate measure of amounts ingested. Animal matter may be overestimated by SIA and video analysis. At Bahia de los Angeles, Mexico, depending on sampling technique, animal matter was found to comprise 3% (oesophageal lavage), 20% (gut content) and 32% (video) (Seminoff et al. 2002; Seminoff et al. 2006). Similarly, at Shark Bay, Australia, animal matter was measured at 0% (oesophageal lavage), 20% (SIA), and 40-43% (video) (Burkholder et al.

2011; Thomson et al. 2018). It would be interesting to conduct simultaneous studies using multiple methods at other sites to confirm whether such relative differences are consistent.

In contrast to traditional gut sampling, SIA analyses have teased apart some of the cryptic components of green turtle diet. In the Caribbean, Vander Zanden et al. (2013) reported that while green turtles in Costa Rica might appear to have a more omnivorous diet (due to presence of higher δ15 values) than foraging aggregations in neighbouring Nicaragua, in fact, differences in stable isotope composition were attributable to regional variation in primary production and nutrient cycling rather than differences in patterns of prey consumption (Vander Zanden 2013). Another limitation of SIA is that all prey items must be sampled within the same time frame that the sampled tissues are synthesised (Haywood et al. 2019). It follows that stable isotope studies that only sample potential prey items previously identified in gut or lavage samples taken at a foraging site risk excluding important prey items. For example, in Bermuda, samples of seagrass, macroalgae and certain potential prey animals were analysed to determine stable isotope ratios (Burgett et al. 2018). But, because the diet studies had not identified mangroves in their lavage samples, stable isotopes of mangroves were not assessed even though it is possible that mangroves which occurred in the area actually featured in the diet. Sampson et al. (2018) reported they were unable to run the MixSIAR model for green turtles due to exclusion of key prey items that were not considered potential prey from previous lavage studies.

Climate change considerations

Our study concludes that SST has a small but significant effect on levels of omnivory, and so a warming climate is likely to modify the prey available to green turtles. There is some evidence that recent changes in forage availability are associated with changes in water temperature, particularly in shallow waters where summertime superheating can lead to major loss of temperature-sensitive seagrasses (Campbell et al. 2006). For example, a major die-off of colder-water seagrass species occurred in response to a marine heatwave that impacted the important green turtle foraging area in Shark Bay, Western Australia (Arias-Ortiz et al. 2018).

Future changes in local conditions (e.g. SST, sea level, salinity or water current regime) may modify ecosystem structure and biodiversity (Thomson & Heithaus 2014). An overall reduction in seagrass habitat globally has been predicted during the next decade due to a combination of anthropogenic threats (Unsworth et al. 2019). Climate change might alter patterns of oceanic currents, gyres and eddies (Toggweiler & Russell 2008) and thereby affect water temperature and the availability and distribution of sea turtle food resources. Moreover, habitats are rarely static through time and can undergo long-term natural cycles of loss and recovery (Rasheed & Unsworth 2011) influencing their capacity to support grazing turtles.

Our review indicates that green turtle diets are variable, and this flexibility may enable adaptation to changing resources after environmental perturbations such as marine heatwaves (Arias-Ortiz et al. 2018). Turtles may adapt to seasonal changes in food availability by modifying their diets (González Carman et al. 2012). Green turtles can alter their feeding behaviour as evidenced by consumption of invasive seagrass species that spread into key foraging habitats (e.g., Becking et al. 2014; Whitman et al. 2019). Turtles might also expand their foraging home ranges, as they have with serial residency in Shark Bay, Western Australia (Thomson et al. 2018). Or they may shuttle between foraging sites (Piovano et al. 2019) or even adapt to new foraging sites, as demonstrated by a loggerhead turtle that re-located to a new site after flooding and a tropical cyclone destroyed > 1000 km² benthic habitat in its home range (Shimada et al. 2020).

Flexibility in green turtle diet is evident across regions. Temporary diet switching between seagrass and macroalgae has been recorded by individual green turtles (Fuentes et al. 2006) and longer-term diet shifts in response to invasive algae have been observed in turtle aggregations (Russell & Balazs 2015; Christianen et al. 2019). Likewise, green turtles have adapted their diet to changing environments through seasonal variation in diet (Piavano et al. 2020) and switching between reef and estuarine habitats (Machovsky-Capuska et al. 2020). At the extremes of their geographic distribution along the South American Atlantic coastline, the foraging plasticity of green turtles is demonstrated by an omnivorous diet and pelagic foraging (Santos et al. 2015). Green turtles are highly adaptive, but whether turtles will be able to sufficiently shift their diet in response to warming SST remains a concern for this threatened species. In conclusion, ours is the first study to document the full extent of variation in green turtle diet in different regions throughout the world, and to quantify this relationship on a global scale. We were also able to demonstrate a correlation between water temperature and diet composition, which has important implications in the face of climate change.

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CHAPTER THREE: Nest site selection in sea turtles shows consistencies across the globe in the face of climate change

This chapter was amended from published work:

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Disclaimer: GCH and NE conceived the project. HJS and NE completed the fieldwork. HJS led the data compilation and analysis. GCH and HJS led the writing with contribution from all authors.

ABSTRACT

Sea turtles face a risk of extinction due to climate change causing warming of nests, which may both increase sex ratio skews, with fewer males being produced, as well as increasing embryo mortality in nests. In theory, these threats could be mitigated by turtles switching their nest sites to cooler locations on beaches. We assessed nest positioning for green turtles (*Chelonia mydas*) in the Chagos Archipelago, a major nesting site in the Indian Ocean, and showed that nests were generally (90% of all nests) in vegetation at the back of the beach, where the risk of sea water inundation was lowest. The 10% of nests on the open beach were close (mean -1.5 m) from the vegetation. Sand temperatures at nest depths were similar across three beach zones (open sand, edge of vegetation, within the vegetation). Nest positioning was reviewed for 51 studies at 53 sites (including the current study) across the globe and across seven species: green turtles, hawksbills (*Eretmochelys imbricata*), loggerheads (*Caretta caretta*), leatherbacks (*Dermochelys coriacea*), olive ridleys (*Lepidochelys olivacea*), Kemp's ridley (*Lepidochelys kempii*) and flatbacks (*Natator depressus*). Both in the Chagos Archipelago and across the globe studies show turtles generally tend to crawl a sufficient distance to minimise sea water over-wash of nests, which can kill embryos. Hence maximising embryo survival, rather than considerations of hatchling sex ratios, seems to be the main driver for nest positioning and so we conclude that sea turtles are, generally, unlikely to switch to select cooler beach sites to mitigate climate warming.

KEYWORDS

climate change; feminisation; hatchling sex ratio; marine turtle; nest location; plastic pollution; sea level rise; temperature-dependent sex determination; trade-off

INTRODUCTION

Across the globe the ability of animals and plants to mitigate climate warming impacts may be key to their future survival, through for example, range changes or phenological shifts in the timing of breeding and migrations (Charmantier and Gienapp 2014). For oviparous species, including birds, reptiles and fish, the thermal environment eggs are exposed to, may have important implications for offspring survival (Feiner et al. 2016; DuRant et al. 2019; Martin et al. 2020) and so a potential avenue to mitigate climate warming in these taxa is through the selection of cooler sites for egg laying. For some species there is good empirical evidence that the egg laying site may be selected based on their thermal environment, such as in some birds (Bison et al. 2020). However, for other taxa it is equivocal if the likely thermal environment for developing eggs plays a role in the selection of sites for egg laying.

For sea turtles there are particular concerns about climate warming since the group has temperature dependent sex determination, with female hatchlings produced at warmer incubation temperatures and vice versa. Future warming may lead to increasingly female skewed populations and, potentially, single sex populations and then extinction (Godley et al. 2001; Hawkes et al. 2009; Witt et al. 2010; Jensen et al. 2018; Booth et al. 2020; Hays et al. 2023). Concern surrounding this scenario has been exasperated by the finding that the majority of nesting populations already produce heavily female biased hatchling sex ratios (Broderick et al. 2000; Booth and Freeman 2006; Fuentes et al. 2009; Laloë et al. 2016). With sea turtles, several studies have now suggested that phenological shifts in the nesting season will be insufficient to mitigate climate warming (Monsinjon et al. 2019; Laloë and Hays 2023), which has re-invigorated studies of nest site selection and how preferred nest sites could influence incubation conditions and primary sex ratios (Kamel and Mrosovsky 2006; Heredero Saura et al. 2022).

Given this interest in nest site selection, here we assess the nest positions for green turtles (*Chelonia mydas*) at a major rookery in the Indian Ocean where a balanced hatchling sex ratio has previously been reported (Esteban et al. 2016). Further, we explore potential drivers of nest site selection based on the various hypotheses that have been proposed, including that turtles might select sites close to vegetation behind beaches, might select sites at a certain distance or height above the water line or might simply randomly lay clutches across the width of beaches. Further we embed our finding in a synthesis of the previous studies around the world to draw out a consensus for the key processes that seem to drive nest site selection for nesting populations across the globe.

METHODS

The study site was located on Diego Garcia which has 40 km of beach suitable for nesting turtles and is the largest atoll in the Chagos Archipelago, where an estimated 20,500 green and 6,300 hawksbill turtle (*Eretmochelys imbricata*) clutches are laid annually (Mortimer et al. 2020). Green turtles nest year-round, mostly between June and October with a peak in August, and hawksbill turtles nest between October and February (Mortimer et al. 2020). A 2.8 km index beach (Fig. 3.1a) was selected for turtle nesting research as it hosts some of the highest densities of nesting activity identified, is partially located in the Diego Garcia Ramsar Site and is easily accessible (Mortimer et al. 2020). Foot patrols were conducted in 2021 and 2022 including daytime surveys (start time ranged from 0500-1500 hr) to count recent turtle activities (tracks, nests) and nighttime surveys (dusk till dawn) in search of nesting females to directly observe nesting activity to record clutch counts, biometrics, and nest measurements. The following measurements (using a flexible transect tape in metres) to the nest were recorded; crawl distance (from sea to nest), high water line (HWL) to nest, HWL to vegetation line, sea to nest (straight distance), sea to vegetation line, vegetation line to nest (negative values are nests in front of the vegetation line towards the sea). The high water line was defined as the boundary between dry and wet sand and debris markings left by the last high tide. For some nests in 2022, crawl distances were measured at night from the water’s edge as soon as the track was encountered, i.e., within 2 h of the turtles emerging onto the beach. Not all measurements were recorded for all nests and so the sample sizes vary for each analysis. A straightness index (SI) was calculated from the straight distance to the nest from the sea divided by the total distance of the crawl from the sea to the nest.

In 2021, we measured heights of nests above MHW encountered in February and at nest sites recorded in 2018 and 2019 during peak nesting season (June-July) that were revisited using GPS coordinates. In 2022, we measured the height of recent nests that we encountered and marked between June and September. We used a theodolite (Automatic Level AL8-26, Model 8926, David White, USA), transit surveyor's tripod (model 1228, Lietz, USA) and a four-meter pole marked at 0.5 cm intervals to measure the height of nests versus the recent neap HWL on the 19-20 February 2021 and 22 September 2022. Nest sites were recorded between February and September and the majority of sites were recorded during peak nesting season including June-July 2018, June-July 2019, February 2021 and June-September 2022. Nests located in 2018 and 2019 were measured in 2021 along with recent nests from February 2021 and recent nests in 2022. The tripod height was subtracted from the total height and the neap high tide height (from National Tidal and Sea Level Facility, 2021, 2022) was added to obtain nest height above chart datum. We calculated the mean high-water (MHW) height across the months of February 2021 and September 2022 and subtracted values from our nest height above chart datum for each survey month respectively to obtain nest height above MHW (Fig. 3.1b).

Sand temperature at 50 cm was measured at three locations along the nesting beach. 50 cm depth was chosen as this depth covers both hawksbill and green turtle nest depths and allows comparison to previous sand temperature studies at this site where buried temperature loggers have been placed at 30 cm, and 50 cm to estimate hawksbill conditions and 50 cm, and 70 cm to estimate green turtle conditions (Esteban et al. 2016). The three sampling zones (Fig. 3.1) were determined by observations of frequent green turtle nesting locations. At each location the sand temperature was measured several metres into the vegetated zone (where nesting occurred indicated by presence of body pits), at the edge of vegetation zone and in the open beach zone a few metres from the vegetation and above recent HWL. Initial trials using a temperature probe and data logger (1 m long Compost Probe PB-5013-XM with a Tinytag View 2 TV-4020, Gemini Data Loggers, UK, accurate to 0.35 °C) were conducted at 30, 50 and 70 cm depths to test stabilisation time of the sand temperature at different depths.

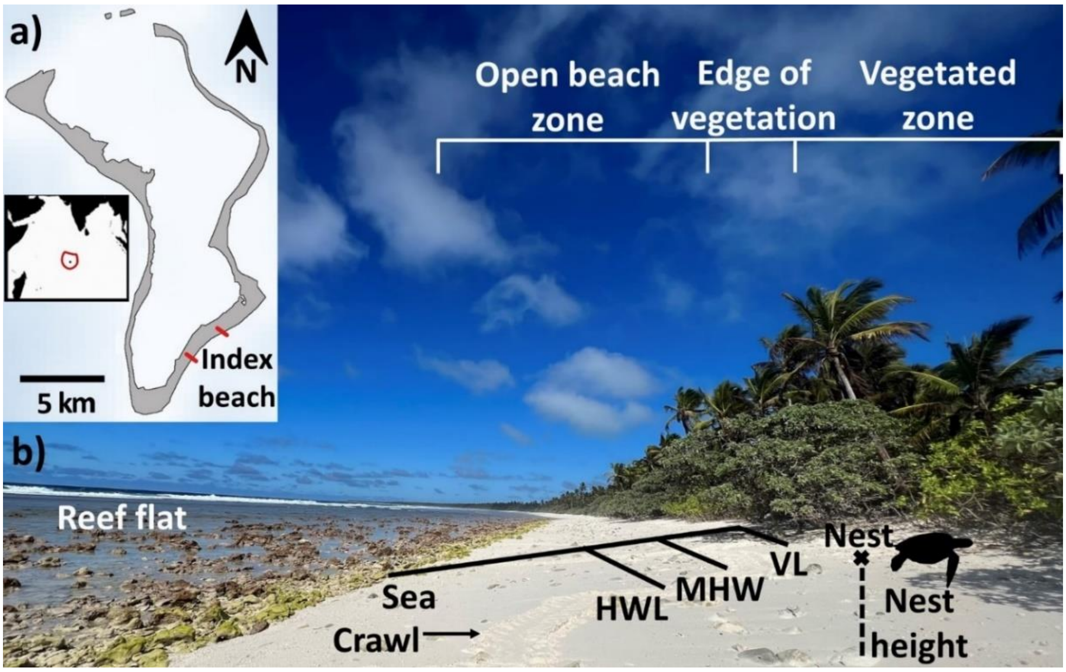

Figure 3.1. a) Diego Garcia (land shaded grey) and the index beach (indicated by the red lines) with a map showing the location of the Chagos Archipelago in relation to the wider Indian Ocean (red boundary = Marine Protected Area). **b)** Beach profile showing the measurements taken from the nest (Vegetation Line, VL; High Water Line, HWL; Sea; Crawl; Nest Height). Mean High Water, MHW was calculated (using National Tidal and Sea Level Facility, 2021, 2022) for estimation of Nest Height.

Stable temperatures occurred quicker at greater depths. At 50 cm depth the temperature stabilised within three minutes. For the study, the probe remained in the sand for three minutes before a reading was recorded. The probe was placed in cold water in an insulated bottle between each sample point and temperature was recorded for a calibration check. We took three measurements in each beach zone at each sampling location along the beach in March and September 2021 and in July and August 2022. In March 2021 and July 2022, repeats were conducted over three consecutive days. We aimed to measure sand temperature as close to neap tides as possible and during dry periods to avoid over-wash and heavy rainfall influencing measurements.

A literature search was conducted in March 2023 for papers on nest site selection of sea turtles. We conducted a search on Web of Science using the search term: ALL = ("Sea turtle") AND ALL = ("Nest site selection"). For relevant papers, we made note of the species, location of study, nest zone preference (e.g., vegetation zone, in front of vegetation zone or in the open sand zone).

RESULTS

Nest positioning

Nest sites were generally in the vegetated zone that backed the nesting beach (Fig. 3.2a). For example, 43 of 48 nests (90%) were 0-9.55 m into the vegetation and only 5 of 48 nests (10%) were on the open beach zone before the vegetation. Even these few nests on the open beach were close (mean -1.5 m) to the vegetation.

There were typically only a few metres between the HWL and vegetation line (mean = 2.56 m). When the distance from the HWL to the vegetation was further, nests tended to be further from the HWL as turtles needed to traverse more open sand before entering the vegetation zone (Fig. 3.2b). All nests were above the MHW (range = 0.14 – 2.44 m; mode = 1.35 m; Fig. 3.2c).

As the crawl distance to a nest increased, nests tended to be further into the vegetation, although there were longer crawls where nests were on or just within the vegetation. Sometimes turtles encountered vegetation that was impenetrable, typically dense stands of native Indo-Pacific shrubs *Suriana maritima* or *Scaevola taccada*. In these cases, turtles then often crawled parallel to the vegetation until they found a break that allowed them to crawl further from the sea and into the vegetation zone (Fig. 3.3a; Fig. 3.3b). So often in these cases the total crawl distance could be very long (up to 76 m), even though these long crawls did not lead nests to be further into the vegetation (Fig. 3.3c). Rather, these long crawls were simply due to the circuitous crawl path along the vegetation line, before the turtle was able to enter the vegetation and nest. Most (66%) nests had no preceding aborted digging attempts, but 24% and 10% of nests had one or two preceding aborted attempts respectively. These nesting attempts were aborted because of material (typically roots or plastic macrodebris) impeding digging. These aborted digging attempts followed the same spatial distribution as nests, typically being within the vegetation zone.

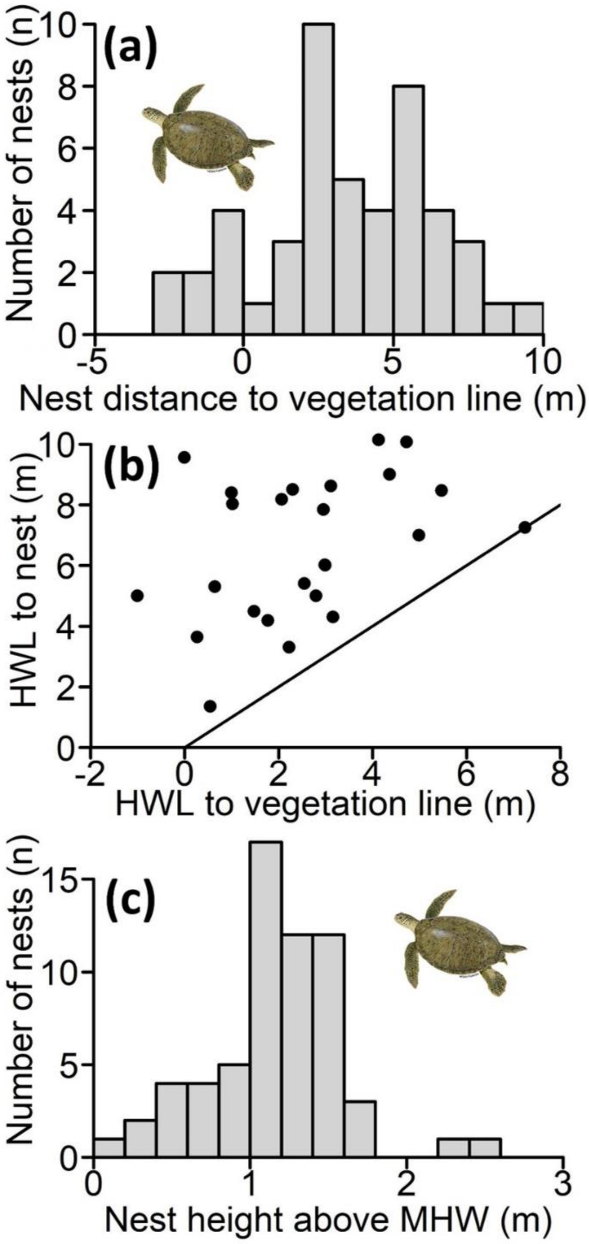

Figure 3.2. a) the distribution of nests with respect to the vegetation line *(n* = 48*).* **b)** The link between the distance from the high-water line (HWL) to the vegetation and the HWL to the nest to show that turtles tended to crawl further when the sea was further from the vegetation line (*n* = 25). Black line = line of equivalence. **c)** The frequency distribution of nest heights above the mean high water (MHW; calculated for the month the survey was conducted using National Tidal and Sea Level Facility, 2021, 2022*; n* = 61). Data sources: a) and b) *in situ* track surveys, c) theodolite measurements from marked nest locations. The turtle image was provided by NOAA Fisheries (www.fisheries.noaa.gov).

Sand temperatures and nest position

The mean daily sand temperature recorded at 50 cm depth at three sites in the vegetated zone was 26.87 °C (SD = 1.10 °C, range = 25.70-28.60 °C, n = 24). Sand temperatures at 50 cm depth was similar across the three beach zones (open beach, edge of vegetation, vegetated zone) and not significantly different (ANOVA: $F_{2,69} = 0.81$, $P = 0.45$). For example, the temperature at nest depth within the vegetated zone was, on average, only 0.48 °C cooler than on the edge of vegetation and 0.03 °C cooler than in the open beach zone (Fig. 3.4).

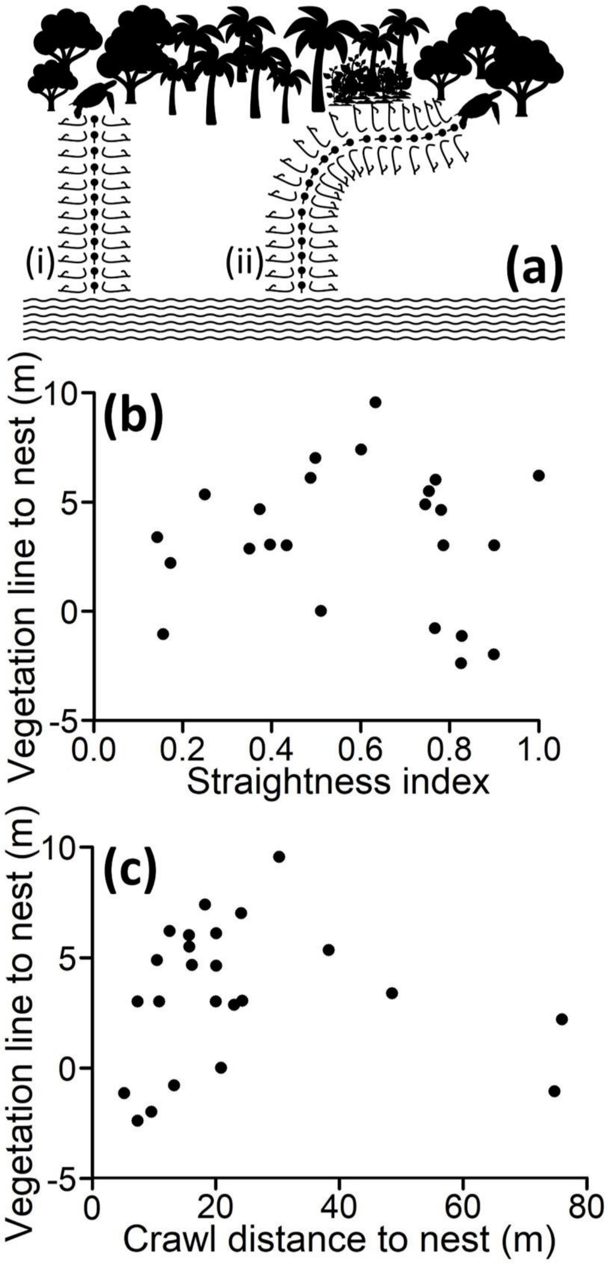

Figure 3.3. **a)** Schematic of different crawls from the sea, (i) an example where a turtle crawled directly into the vegetation and (ii) an example where the turtle initially could not enter the vegetation as it was too dense and then crawled parallel to the vegetation line for some distance. **b)** Relationship between the straightness of the crawl to the target (nest) and the distance of the nest to the vegetation. Nests remain close to the vegetation line and into the vegetation regardless of straightness of movement to the nest. **c)** Relationship between the crawl distance to the nest from the water's edge versus the distance of the nest to the vegetation line.

Studies across the world

We found 50 studies around the world (excluding the current study) that had reported nest site selection for sea turtles at 52 sites (Fig. 3.4). In general, studies found that nests tend to be distributed above the HWL. For some nesting beaches, where there was vegetation behind the beach, turtles tended to nest in the vegetation zone.

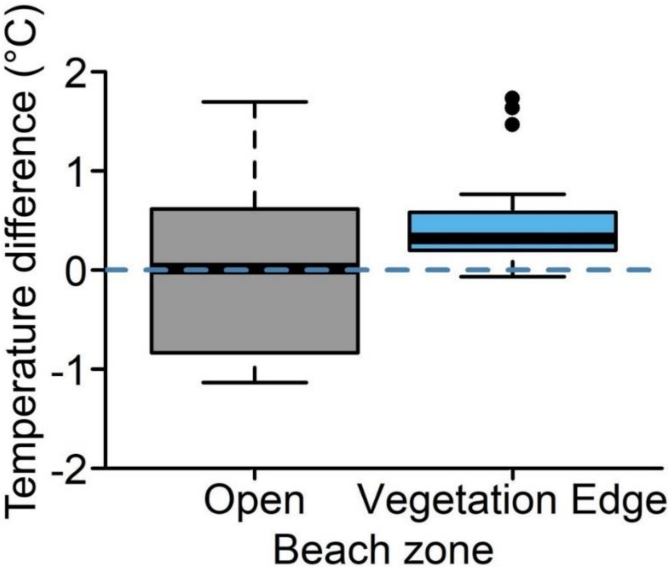

Figure 3.4. Temperature variation of the vegetation edge and open zones on the index beach, Diego Garcia, when compared to the vegetated zone as a reference. Bold horizontal lines indicate the median and boxes the 25th and 75th percentiles; the whiskers indicate the values within 1.5 times the interquartile range and the circles are outliers.

In other cases, the vegetation tended to provide a constraint on the inland crawl distance, with turtles nesting in front of the vegetation. In other cases, where there was no vegetation behind the beach or the vegetation was very distant from the sea, then crawl distances can be very long, and turtles seemed to position nests above the HWL but short of the vegetation. Across the studies, the consensus was that turtles position nests well away from the sea to reduce the risk of sea water inundation which could result in nesting into vegetation on narrow beaches.

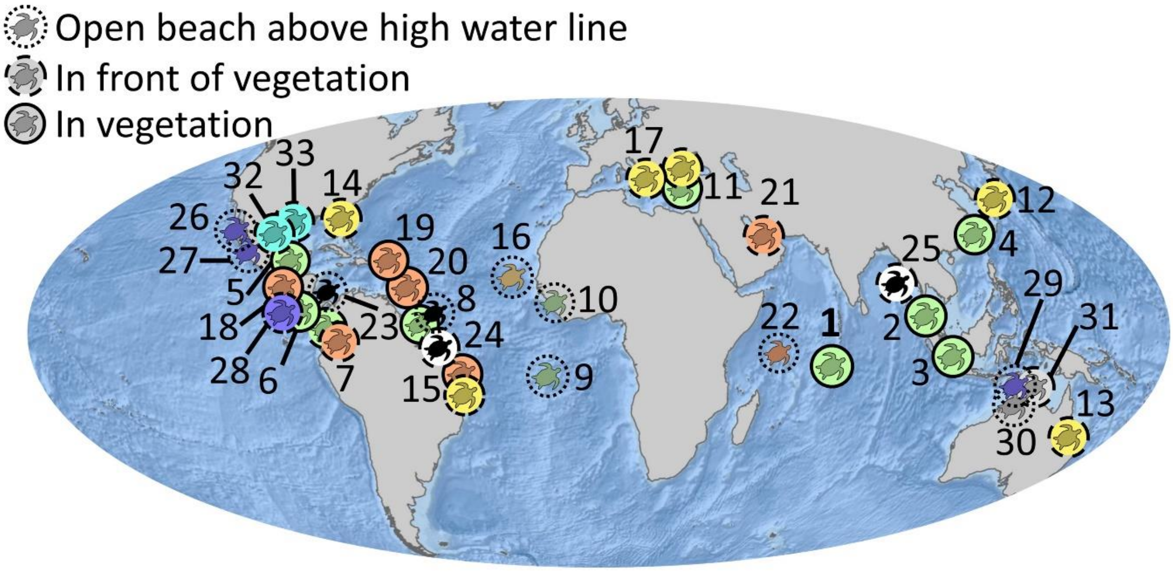

Figure 3.5. Studies around the world where the distribution of sea turtle nests has been recorded (Table S3.1). Filled symbols with full circle indicate nesting mainly in the vegetation zone; filled symbol with a dashed circle indicate nesting mainly on the open beach in close proximity to the vegetation line; open symbols with dotted circle indicate nesting on the open beach above the HWL but short of vegetation. Green = green turtle, yellow = loggerhead turtle, red = hawksbill turtle, purple = olive ridley, black = leatherback turtle, grey = flatback turtle, blue = Kemp's ridley turtle. Green turtles: **1** = this study, 2 = Malaysia (Sarahaizad et al. 2012; Mohd Salleh et al. 2018; Mohd Salleh et al. 2021), 3 = Indonesia (Rumaida et al. 2021), 4 = Taiwan (Wang and Cheng 1999; Chen et al. 2007), 5 = Mexico (Zavaleta-Lizárraga and Morales-Mávil 2013; Santos et al. 2017), 6 = Costa Rica (East Pacific green turtles; Heredero Saura et al. (2022)), 7 = Ecuador (Carpio Camargo et al. 2020), 8 = Suriname (Whitmore and Dutton 1985), 9 = Ascension Island (Hays et al. 1995), 10 = Guinea-Bissau (Patrício et al. 2018),

11 = Turkey (Turkozan et al. 2011). Loggerhead turtles: 11 = Turkey (Kaska et al. 2010; Turkozan et al. 2011), 12 = Japan (Hatase and Omuta 2018), 13 = Australia (Kelly et al. 2017), 14 = USA (Hays et al. 1995; Salmon et al. 1995; Garmestani et al. 2000; Gravelle and Wyneken 2022), 15 = Brazil (Serafini et al. 2009), 16 = Cape Verde (Martins et al. 2022b), 17 = Greece (Hays and Speakman 1993; Karavas et al. 2005). Hawksbill turtles: 18 = El Salvador and Nicaragua (Liles et al. 2015), 7 = Ecuador (Carpio Camargo et al. 2020), 19 = Guadeloupe (Kamel and Mrosovsky 2005), 20= Barbados (Horrocks and Scott 1991), 15 = Brazil (Serafini et al. 2009; Santos et al. 2016), 21 = Qatar and Iran (Ficetola 2007; Zare et al. 2012; Nasiri et al. 2022), 22 = Seychelles (Gane et al. 2020). Leatherbacks: 23 = Costa Rica (Spanier 2010; Neeman et al. 2015), 8 = Suriname (Whitmore and Dutton 1985), 24 = French Guiana (Caut et al. 2006), 25 = India (Sivasunder and Devi Prasad 1996). Olive Ridley: 26 = Mexico (López-Castro et al. 2003), 27 = Mexico (Hart et al. 2014), 28 = Costa Rica (Ávila-Aguilar 2015), 29 = Australia (Blamires and Guinea 1998). Flatback turtle: 30 = Australia (Blamires et al. 2003; Bannister et al. 2016), 31 = Australia (Hope and Smit 1998). Kemps ridley: 32 = Mexico (Márquez 1994), 33 = USA (Culver et al. 2020).

DISCUSSION

For sea turtles the nest position may have important implications for survival and sex of embryos. Of concern across nesting beaches is the fact that repeated salt-water inundation of nests will kill developing embryos due to both the osmotic impact of salt in the nest as well as removal of oxygen spaces within the sand and the resulting drowning of embryos (e.g., Ackerman 1997; Wood and Bjorndal 2000; Pike et al. 2015). Hence many studies have reported that hatching success (the proportion of eggs resulting in a hatchling emerging from the sand) tends to increase in nests further from the sea (Hays and Speakman 1993; Patrício et al. 2018; Martins et al. 2022b; Whitesell et al. 2022). Our key finding that green turtles tend to position their nests within the vegetation behind beaches, and hence as far from the sea as possible, even if this necessitates circuitous crawls to get to those nest positions, suggests these turtles are trying to minimise the likelihood of salt-water inundation of their nests. The nesting beaches on Diego Garcia may be particularly prone to over-wash as they are relatively narrow, with typically only a few metres between the HWL and the vegetation. So, at this site it may be particularly important for turtles to crawl into the vegetation to minimise nest inundation. A similar pattern of nesting in supralittoral vegetation far from the sea has also been reported for other green turtle nesting beaches around the world. For example, Mexico (Zavaleta-Lizárraga and Morales-Mávil 2013), Suriname (Whitmore and Dutton 1985), and Costa Rica (Heredero Saura et al. 2022) as well as in hawksbill turtles nesting, for example, in Brazil (Serafini et al. 2009), and Guadeloupe (Kamel and Mrosovsky 2005), and olive ridley turtles in Costa Rica (Ávila-Aguilar 2015). In contrast, at some nesting beaches there may be a lack of supralittoral vegetation and so vegetation cannot be a constraint on the inland crawl distance. For example, at the major green turtle rookery on Ascension Island, supra-littoral vegetation was historically very sparse or non-existent and there, green turtles have been shown to crawl long distances from the sea before nesting (up to many 10s of metres), crawling until they reach soft sand above the HWL (Hays et al. 1995). Similarly, on wide beaches in Guinea-Bissau, West Africa, green turtles crawl long distances from the water to nest either at the back of beach or in supralittoral vegetation (Patrício et al. 2018). Additionally, a comparison of individual nesting beaches in Penghu Archipelago, Taiwan, found turtles nest in the open or interface zones when the vegetation was further inland, but when the open beach zone was narrower, nests were located more in the interface and vegetated zones (Chen et al. 2007).

Loggerhead turtles tend to show similarities to green turtles in that nests tend to be positioned far from the sea to minimise inundation, but at the same time loggerheads often tend to nest just in front of supralittoral vegetation rather than in the vegetation zone. This pattern of nest placement has been observed, for example, with loggerheads nesting in Brazil (Serafini et al. 2009), Greece (Hays and Speakman 1993; Karavas et al. 2005), and Japan (Hatase and Omuta 2018). Very few studies were found for Kemp's ridley turtles, but they are also shown to nest far from the sea but in front of vegetation in Mexico (Márquez 1994) and Texas, USA (Culver et al. 2020). This pattern of nesting just before reaching vegetation may be because roots can impede digging with this smaller species and may lead to nesting attempts being aborted (Hays et al. 1995). Although, this may likely be dependent on site and the availability of open nesting habitat. These nest positioning strategies seem to work well, with a dramatic increase in nesting numbers following the introduction of measures to reduce poaching of nests (Mazaris et al. 2017; Hays et al. 2022a), i.e. over-wash of clutches may not impede population recoveries. However, this largely depends on the amount of over-wash and with increasing sea level rise and storms, over-wash could become of increasing concern (Rivas et al. 2023). Similarly, Gravelle and Wyneken (2022) showed nest location variation based on microclimate, where subtropical loggerhead nests were primarily in the mid-beach zone on flat and wide beaches which had high emergence and hatchling success compared to warm temperate nest sites situated on narrow beaches with nests clustered at high elevations by the base of the dune. For loggerheads nesting in Boa Vista (Cape Verde), Martins et al. (2022b) reported that turtles crawled long distances away from the sea to nest, but preferentially nested in the middle of the beach, avoiding nesting both close to the tideline and close to the vegetation line, however, due to the low elevation profile at this study site and the fact that predation occurs across the whole beach profile, the risk of inundation and predation was high regardless of nest location.

Like loggerheads, olive ridley turtles nest in front of the vegetation line but they nest anywhere between the HWL and vegetation line. In Mexico, Hart et al. (2014) found turtles preferred nesting on the open beach from the berm to the vegetation line. Likewise, López-Castro et al. (2003) found nests from 3-41.5 m from the tide line with the majority (58%) 10-20 m above the tide line. In the South Pacific region of Costa Rica, turtles were found to nest between the HWL and vegetation line but showed a stronger preference for nesting as far from the tide line as possible, even if this meant closer to the vegetation where there was higher risk of predation and a further crawl for the nesting female and hatchlings to reach the sea (Ávila-Aguilar 2015).

While there are many studies, reviewed above, that have examined nest positioning and the implications for embryo survival, fewer studies have considered the sensory processes that might drive nest site selection. Some earlier work suggested that turtles start digging when they perceive a decrease in surface sand temperature (Stoneburner and Richardson 1981). However, several subsequent studies have cast doubt on this assertion. On some beaches any perceived change in sand temperature at the sand surface is likely linked to the sand texture and a switch from compacted over-washed sand below the HWL to drier, “fluffier” sand above the HWL where turtle flippers sink a little deeper as they crawl. So, sand texture might provide turtles with a cue to sense they have crawled above the HWL (Hays et al. 1995). This change in sand texture may occur, for example, with green turtles nesting on Ascension Island where crawl distance is linked to the distance from the water’s edge to the HWL with turtles likely only attempting to nest when they perceive this discontinuity between over-washed compacted sand and dry uncompacted sand (Hays et al. 1995). Similarly, Wood and Bjorndal (2000), working with loggerhead turtles in Florida, concluded that sand surface temperature alone was unlikely to be a cue to initiate nesting but might be used as one cue among others to detect when the crawl inland was far enough to reduce inundation. Through a process of simply perceiving when the HWL has been reached, and so a beach zone has been reached that has less chance of over-wash, turtles might set the lower limit on the beach for where they nest. In contrast, where there is supralittoral vegetation behind beaches and the distance from the water to the vegetation line is relatively short, turtles might simply tend to crawl until they reach (loggerheads, olive ridleys, Kemp’s ridley, flatbacks, *Natator depressus*) or enter (green and hawksbill turtles) the vegetation zone before they start digging. So, again, on these types of nesting beach with supralittoral vegetation, a simple sensory process might be involved in nest site selection. Turtles might often follow simple rules: crawl a certain distance until you perceive (e.g., sand texture) that you are above the HWL and/or constrain your crawl and nest when/if you encounter vegetation. Such a simple decision-making process may explain why turtles sometimes nest on the open sand (i.e., they have crawled far enough to perceive they are above the HWL), sometimes nest just before vegetation (i.e., the vegetation constrains their inland crawl as in the case of loggerheads) or inside the vegetation (as in the case at some green and hawksbill nesting sites). The outcome of this simple decision-making process would be that regardless of vegetation behind beaches or not, or the distance from the water to the vegetation line, turtles will minimise the risk of nest inundation. Through these processes of nest site selection, a tendency for turtles to nest a certain height above the sea level (e.g., this study but also widely reported such as for loggerhead and green turtles (Wood and Bjorndal 2000; Maurer and Johnson 2017; Patrício et al. 2018) might simply be an emerging property of other decisions driving nest site selection.

Our results for the drivers of nest site selection suggest that this process is unlikely to be an avenue that might help mitigate climate warming across populations. The picture emerging from studies around the world is that turtles tend to select nesting sites where the chances of sea inundation are low. At the same time, turtles do not continue to crawl indefinitely inland even if there is not vegetation to constrain their crawls, as then hatchlings emerging from nests further inland may have problems locating and reaching the sea (Kamel and Mrosovsky 2004). There is also some evidence that experienced nesters may nest in beach zones less prone to inundation than first-time nesters (Pfaller et al. 2009), i.e. as they nest more times turtles learn more about the physical make up of beaches and how far they can crawl inland. While generally turtles do not seem to select sites based on the likely incubation temperatures, there might be some sites where individual turtles differ in their selection of microhabitats and tendency to nest in cooler shaded areas versus warmer unshaded areas, as has been suggested for hawksbill turtles in the Caribbean (Kamel and Mrosovsky 2005) and green turtles in West Africa (Patrício et al. 2018). In these cases, one possibility is that if nest site selection is a heritable trait, which is unknown, future nest site selection may bias towards shaded sites resulting in cooler nests.

However, there is no evidence that this scenario might apply, with selection of nesting sites that minimise nest inundation seeming to dominate across the globe.

There was only a relatively small difference in sand temperature at nest depths between beach zones but even these small differences might impact hatchling sex ratios. For example, the mean temperature on the open beach zone was 0.45 °C cooler than the mean temperature on the edge of the vegetation zone and the mean temperature on the vegetated zone was 0.48 °C cooler than the mean temperature on the edge of the vegetation zone. Using a generic sand temperature versus hatchling sex ratio curve (Hays et al. 2017), this difference in sand temperatures between zones might change the hatchling sex ratio (% females) by up to 15.7% for those nests close to the pivotal temperature where hatchlings of both sexes are produced.

While green, hawksbill, olive ridley, Kemp's ridley and loggerhead turtles seem to generally nest either in vegetation or high on the beach, often in front of vegetation, based on the presence or absence of vegetation and its distance from the sea, leatherback turtles have been suggested to position nests differently. Older reports suggested a strong tendency for leatherbacks to nest on the open sand and often below the HWL, reporting that around 30% of nests were below the HWL for leatherback nesting in French Guiana, Suriname, and South Africa (Mrosovsky 1983). It was suggested that beach erosion and over-wash on leatherback nesting beaches may be difficult to predict as they often nest on high-wave energy beaches and so there may be poor links between nest placement and embryo survival (Mrosovsky 1983). However, Spanier (2010) and Neeman et al. (2015) found that for leatherbacks nesting on the Caribbean coast of Costa Rica, while nests tended to be laid on the open beach rather than in vegetation, turtles still avoided nesting below the HWL where the risk of inundation was highest, although nests were closer to the HWL than the vegetation line. Similarly, Caut et al. (2006) reported that for leatherbacks nesting in French Guiana, most nests were at the back of beach in front of vegetation. It may be that other factors drive the tendency for leatherbacks not to nest within the vegetation zone, such as their softer carapace, compared to other species, which makes them less resistant to abrasions or like loggerhead turtles, they may struggle to dig nests in vegetated areas due to roots impeding their digging or due to their size making it difficult to carry themselves further up the beach.

Localised beach characteristics may also play a part in nest site selection for locations where leatherbacks nest. For example, dune scarps caused by beach erosion influence nest site selection in leatherbacks at Pacuare Nature Reserve, Caribbean Costa Rica as Rivas et al. (2018) found dune scarps created a barrier on the nesting beach and around a quarter of the turtles, regardless of scarp height, would not crawl over them, consequently laying their eggs below the scarps in higher risk areas. This is also the case for flatback turtles at Fog Bay and Bare Sand Island in Northern Australia (Blamires et al. 2003; Bannister et al. 2016). Flatbacks on Bare Sand Island nest at the back of the wider beach on the western side of the island, where there is little to no vegetation, and the constraint of nests is influenced by the elevated sand dunes (Bannister et al. 2016). Similarly, at Fog Bay, flatbacks nest mainly at the dune base and dune slope and very rarely nest on the dune crest (Blamires et al. 2003).

In summary, we have shown that at an important green turtle rookery in the Indian Ocean, as well as many other nesting sites around the world, sea turtles seem to select nesting sites away from the sea where the probability of nest inundation is minimised. These general findings support the long-standing assertion that maximising hatching survival is the key determinant in nest site selection and so turtles might generally be unlikely to shift their nesting zones within beaches to mitigate climate warming. Even though turtles seem to generally crawl inland until the chances of nest inundation are low, a concern with climate change and sea level rise is that loss of nesting habitat, particularly for low lying atolls, will mean turtles are unable to nest in safe beach zones (Rivas et al. 2023). How beaches respond to sea level change is therefore an important question and, in some cases, raising of the beach by redistribution of sand from higher beach areas to lower areas, as is already being implemented at some locations (e.g., Raine Island; Hamann et al. 2022; Smithers and Dawson 2023) may be needed to improve egg survival.

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CHAPTER FOUR: Empirical evidence for the extent of spatial and temporal thermal variation on sea turtle nesting beaches

This work has been submitted to J Therm Biol as:

Stokes HJ, Laloë J-O, Esteban N, Hays GC. Empirical evidence for the extent of spatial and temporal thermal variation on sea turtle nesting beaches.

Disclaimer: GCH, NE, and J-OL conceived the study. GCH, NE, J-OL, and HJS conducted the fieldwork. HJS and J-OL led the data analysis and writing of the manuscript with contributions from all authors.

ABSTRACT

Recording sand temperatures has become routine at many sea turtle nesting sites across the world given the influence of incubation temperatures on hatchling sex ratios. Here we examine empirical sand temperature records across 5 atolls extending 250 km in the Chagos Archipelago, Indian Ocean, between October 2012 and July 2023 and quantify the extent of spatial and temporal thermal variability. Our results suggest that sand temperatures at our study site vary seasonally and inter-annually, between beaches in the archipelago, and within beaches in different nesting habitats. The biggest drivers of thermal variability were seasonal and inter-annual differences, which modulated sand temperatures by up to 3.00°C and 1.03°C, respectively. Intra-beach and inter-beach variability further modulated temperatures by up to 1.01°C and 0.62°C, respectively. In addition, mean monthly sand temperatures were relatively low, suggesting that hatchling sex ratios are fairly balanced. The wide range of sand temperatures recorded at this nesting site suggests that it is likely both male-biased and female-biased clutches are produced during the nesting season. Quantifying thermal variability from a long-term sand temperature time series offers valuable insight into a population with temperature-dependent sex determination and, when possible, should be considered when modelling the effects of temperature on hatchling sex ratios.

KEYWORDS

climate change, endangered species, Marine Protected Area (MPA),
marine turtles, nest site selection, temperature-dependent sex determination

INTRODUCTION

Sea turtles are a widely studied taxon that exhibit temperature-dependent sex determination (TSD), with females being produced at high incubation temperatures. Since the range of temperatures that produce both sexes are relatively narrow (Mrosovsky and Pieau 1991), there are concerns that climate warming is raising incubation conditions around the world and so biasing hatchling sex ratios towards females (Santidrián Tomillo and Spotila 2020). Heightening this concern is the fact that highly female-biased hatchling sex ratios are already being observed around the world (Hays et al. 2014), for example, Raine Island, Australia (Booth et al. 2020) and Ascension Island, Central Atlantic (Godley et al. 2002). A recent evaluation by researchers and managers in the Mediterranean concluded that climate change has the greatest impact on hatchling sex ratios (Mazaris et al. 2023). In light of these concerns, it has become routine to record sand temperatures at sea turtle nesting sites (e.g., Fuentes et al. 2010; Bentley et al. 2020) and gauge whether males are still being produced using biological models (Fuentes et al. 2017).

There are several factors that can influence incubation temperatures at a nesting site, which in turn can lead to a range of temperatures that produce both sexes. First, within a nesting beach the position where the clutch is laid can influence incubation temperature. For example, in French Polynesia the high abundance of tall vegetation at the back of the beach front provides shade that has the potential to cool incubating nests (Laloë et al. 2020). Similarly, shading due to trees fringing the beach decreased nest temperatures at the Mon Repos sea turtle rookery in eastern Australia (Wood et al. 2014). So, clutches that are laid near or within the vegetation incubate at temperatures lower than those laid in the open beach. Second, differences in abiotic factors between beaches can drive differences in incubation temperatures. For example, sand albedo was shown to be a main driver of incubation temperatures on two nesting beaches in Ascension Island, with a dark beach being > 4°C warmer than a light beach (Hays et al. 1995). Similarly, beach orientation affects temperature, and a windward facing Caribbean beach was almost 2°C cooler than a leeward facing beach just 1 km away (Esteban et al. 2018). Third, seasonal variations in temperatures can lead to different incubation conditions throughout the nesting season. For example, low temperatures at the start and end of the loggerhead turtle (*Caretta caretta*) nesting season in the eastern USA were conducive to male production, while higher temperatures in the middle of the nesting season led to the production of females (Mrosovsky et al. 1984). Fourth, nest depth can influence incubation temperatures as findings from olive ridley nesting beaches in Guatemala showed lower sand temperatures at 50cm depth compared to 30cm depth (Ariano-Sánchez et al. 2023). In addition, decreased nest depth in combination with increased clutch size can increase the within-nest incubation temperature range (Houghton and Hays 2001). Finally, differences in annual temperatures can also be a source of thermal variability at a site. For example, years that are exceptionally warm or cold or periods of intense rainfall can lead to the production of a cohort of mainly one sex for one nesting season (Houghton et al. 2007; Hays et al. 2021b).

Given the importance of incubation temperatures on sea turtle population dynamics, here we examine a decade of empirical sand temperatures recorded on nesting beaches in the Chagos Archipelago. We quantify the extent of thermal variability found within beaches, between beaches, within nesting seasons, and between years. In this way we inform on the factors that influence incubation temperatures at sea turtle nesting sites and quantify the range of incubation temperature experienced at this key nesting site. This work uncovers where the capacity for thermal variation lies not only for our study site, but likely also for other sea turtle nesting beaches across the world and offers the possibility to consider thermal variability in a more informed way when modelling the effects of incubation temperatures on hatchling production.

METHODS

Field site

The Chagos Archipelago provides nesting beaches for both hawksbill (*Eretmochelys imbricata*) and green (*Chelonia mydas*) turtles and consists of five atolls comprising submerged banks and islands (Sheppard et al. 2012).

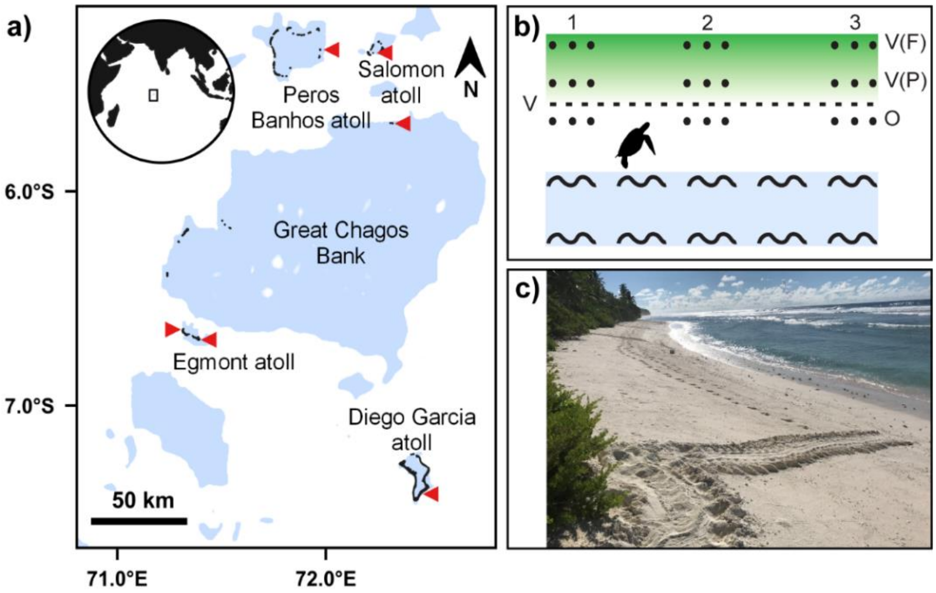

Figure 4.1. a) The Chagos Archipelago. Islands where sand temperature was recorded are indicated by red triangles which span across all five atolls: Diego Garcia (Diego Garcia), Egmont (Ile des Rats and Ile Sudest), Great Chagos Bank (Nelson's Island), Peros Banhos (Petite Ile Coquillage) and Salomon (Ile Jacobin). The inset map shows the Chagos Archipelago (black rectangle) in relation to the wider Indian Ocean. **b)** Schematic showing the temperature probe survey design. Black filled circles represent where the temperature probe readings were taken at three sites (labelled 1, 2, and 3) within three nesting habitats: full vegetation at the back of the beach (V(F)), partial vegetation (V(P)) and in the open beach in front of the vegetation line (O). The dashed line represents the vegetation boundary (V). Green shading indicates the decrease in vegetation cover and shading closer to the vegetation line. **c)** Nesting beach on Diego Garcia showing the available open beach in front of the vegetation and the vegetation boundary. A typical green turtle track is seen in the foreground and three more are seen in the distance.

This study was conducted on six islands across all five islanded atolls in the archipelago (Fig. 4.1a): Diego Garcia (Diego Garcia atoll), Nelson's Island (Great Chagos Bank), Ile des Rats and Ile Sudest (Egmont atoll), Petite Ile Coquillage (Peros Banhos), and Ile Jacobin (Salomon atoll). Nesting beaches are narrow and bordered with a littoral hedge of shrub *Scaevola taccada* (Indo-Pacific native)*, Suriana maritima* and trees including heliotrope, *Argusia argentea,* as well as scattered coconut palms, *Cocos nucifera* (Fig. 4.1c). Nest locations were mainly located under vegetation (90%) and consequently subjected to partial or heavy shading (Stokes et al. 2024). However, some nests were also located in the open beach and received little shading (Esteban et al. 2016; Stokes et al. 2024).

We recorded sand temperatures at sites known to be important nesting areas, as indicated by historic nesting activity (i.e., presence of old body pits along the site; Esteban et al. 2016). To fully represent the extent of nest sites available to turtles and temperatures therein, we recorded temperatures along the beach in different habitats (e.g., in the open beach or in the vegetation) where turtles were observed to nest and at different depths. Two separate but related sand temperature datasets were produced and analysed in this study. With the first dataset collected using buried temperature loggers, we examined temporal, inter- and intra-beach thermal variability using temperature loggers deployed across 11 years. With the second dataset we further explored intra-beach thermal variability using a sand temperature probe on different survey days across two years. Details for each dataset are given below.

Deployment of long-term temperature loggers

Sand temperature was recorded using temperature loggers (Tinytag Plus 2 model TGP-4017, Gemini Data Loggers, UK, dimensions 34 x 51 x 80 mm and weighing 110 g, accurate to less than 0.5°C) buried in the sand at nest depths on Diego Garcia (2.8 km Index Beach), Nelson's Island, Ile des Rats, Ile Jacobin, and Petite Ile Coquillage (Fig. 4.1a). When burying loggers, sand was excavated to the chosen depth using a sand core and then the same sand was replaced back on top of the logger. This process minimises the effects of logger deployment to the natural conditions (see full methods in Esteban et al. 2016). A total of 138 loggers were buried between October 2012 and July 2023 over the course of nine research expeditions. Loggers were deployed at 30cm, 50cm, and 70cm along the beach and in three different nesting habitats (i.e., in the vegetation, in the open beach and at the spring high water line (HWL), which is typically less than a meter from the vegetation). Loggers buried in the same nesting habitat but at different depths were 1 m apart and buried in a line parallel to the high water line. In 2012, at all sites partially shaded in vegetation above the spring high water line one logger was buried at 80cm to record sand temperatures near the maximum green turtle nest depth. Depths were initially chosen based on the range of nest depth recorded for hawksbills (30-45cm; Hitchins et al. 2004a; 45-70cm; Mortimer and Day 1999) and green turtles (70-85cm; Fuentes et al. 2010). To check depth selection criteria, nest depths (from the surface to the top and bottom of nest chamber) were recorded during green turtle nest excavations in 2022. From nest excavations in 2022 we found nest depth to the top of the chamber ranged from 23 to 65cm (mean = 50cm, SD = 13, n = 16) and depth to the bottom of the chamber ranged from 33 to 82cm (mean = 63, SD = 14, n = 16). Loggers were set to record every 4 hr, except for loggers buried in 2019 and 2022 which were set to record every 1 h in order to examine diel thermal cycles in more detail. When processing the temperature data, the first 12 hours of recordings were disregarded from analysis to remove potential thermal fluctuations due to logger deployment.

Sand temperature probe data

Spot sand temperature readings were recorded using a 1 m compost probe (Tinytag View 2 model TV-4020, Gemini Data Loggers with a probe PB-5013-XM). For each measurement, the probe was inserted in the sand at 50cm depth and stabilised for three minutes before the reading was recorded. Temperature was measured along three sites on a nesting beach at Diego Garcia, and Nelson's Island and one site on Ile de Rats and Ile Sudest. At each site, temperatures were recorded within three nesting habitats representative of where turtles nest: vegetation with full shade at the back of the beach (V(F)); a few metres into the vegetation with partial shade (V(P)); open beach in front of the vegetation line (O). Measurements taken at the back of the beach and in the open were approximately 5-10 m apart (Fig. 4.1b).

Sand temperatures collected using the probe were recorded on nesting beaches over 10 survey days at Diego Garcia (15, 16 and 17 March and 3 September 2021, 27, 28, 29 July, and 22 August 2022), Nelson's Island (10 March 2021), Ile de Rats and Ile Sudest (Egmont atoll; 12 March 2021). Survey duration was less than 5 hours at each study site. A preliminary study showed that diel cycles were not affecting our results in this small time window due to low thermal variation over the study period (HJS, unpublished data).

Statistical analyses

We used the long-term sand temperature records (i.e., data recorded between October 2012 and July 2023) to measure inter-annual, seasonal, inter-beach and intra-beach thermal variability. To describe seasonal thermal variation, we calculated mean monthly sand temperatures for each logger, excluding months for which any number of days of data were missing. To examine inter-annual thermal variation, we calculated mean annual sand temperatures from the aforementioned mean monthly sand temperatures. To study the relationship between sand temperature, island (i.e., Diego Garcia vs Nelson's Island vs Ile des Rats vs Ile Jacobin vs Petite Ile Coquillage), habitat (i.e., HWL vs open vs shaded) and depth (i.e., 30cm vs 50cm vs 70cm, vs 80cm), we used the same methods described by Esteban et al. (2016). In short, we removed the effect of seasonality by subtracting the mean sand temperature for all loggers from each individual logger. We then used a simple moving average (N = 10 consecutive daily means) to smooth the data. We used an analysis of covariance on the detrended data to examine the effect of island, habitat, and depth on sand temperature.

We examined diel thermal variation using the long-term temperature loggers that recorded data every hour. In this subset of data, we had sand temperatures from 16 loggers that were buried at 30, 50, or 70cm in the open habitat or in the vegetated habitat. We calculated the difference between the maximum daily temperature and the minimum daily temperature for each day and each logger. We then calculated the mean of those differences, which gives an indication of the average diel thermal variation recorded by each logger. We then performed a two-way ANOVA to examine the effect of depth and habitat on sand temperature.

We further examined intra-beach thermal variability in sand temperatures using the probe data (i.e., data recorded over 10 survey dates in 2021 and 2022). We used linear mixed effects models to understand the effects of habitat, depth, and site on sand temperature. In linear mixed effects models, fixed effects characterised the relationships between the independent variables and the dependent variable, while random effects capture the variations within clusters of data. We entered habitat (i.e., open beach vs partial vegetation vs full vegetation), depth (i.e., 50cm vs 70cm), and site (i.e., different study sites along the same beach) as fixed effects and entered island (i.e., Diego Garcia vs Nelson's Island vs Ile des Rats vs Ile Sudest) and date as a random effect. Likelihood Ratio Tests were used to obtain p-values (Luke 2017). The linear mixed effect models were built in R using the "lmer" function from the "lme4" package (Bates et al. 2015).

RESULTS

Of the 138 temperature loggers deployed between 2012 and 2023, 19 are currently still active on the beach. 94 loggers were recovered as of July 2023. Of these loggers six were broken and recorded no data and two loggers were removed from the analysis due to beach erosion (e.g., loggers were brought to the surface and so did not record at the planned depth). 25 loggers were lost. This study examines sand temperatures for a total of 83 loggers. The longest period of data recorded by a single logger was 1,465 days (mean = 548 days, SD = 223.0 days, n = 83 loggers). Across all loggers, a total of 36,689 days of sand temperature data were obtained.

Temporal thermal variation

Inter-annual thermal variation was apparent in our sand temperature time series with the difference between the warmest mean annual sand temperature and the coolest mean annual sand temperature being 1.03°C. We recorded the coolest sand temperatures in 2021 (mean annual sand temperature = 27.59°C) and the warmest ones in 2015 (mean annual sand temperature = 28.62°C).

In addition to inter-annual variation, seasonal variation was clearly evident in our time series, with sand temperatures increasing in the austral spring and summer and decreasing during the austral autumn and winter (Fig. 4.2). Mean monthly sand temperatures were highest during March and April (mean = 28.77°C, SD = 0.52°C, n = 11 years), and lowest during August and September (mean = 27.02°C, SD = 0.52°C, n = 11 years). The maximum difference between the warmest month and the coolest month of a single year in our study was 3.00°C. Across all years, the mean difference between the warmest month and the coolest month was 1.93°C (SD = 0.48°C, n = 11 years).

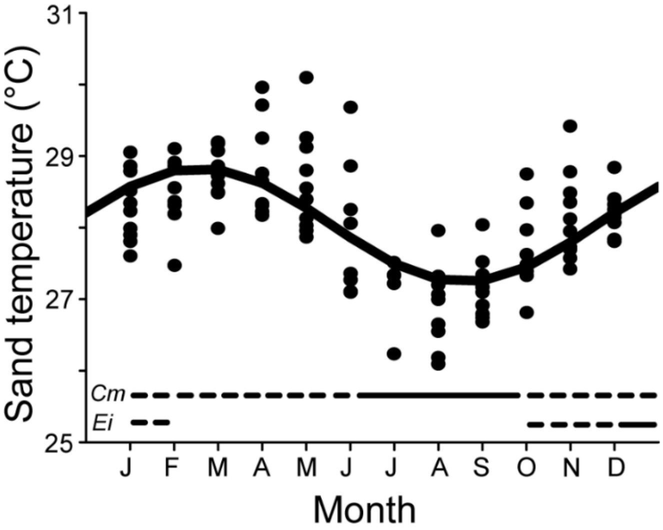

Figure 4.2. Seasonal variations in mean monthly sand temperatures across all years across the archipelago. Each point represents the mean monthly temperature recorded by all loggers in that year. The solid line is the sine fit ($R^2 = 0.46$, $F_{2,107} = 46.11$, $p < 0.01$, n = 11 years). Hawksbill (*Ei*) nesting season (indicated by the dashed horizontal line) occurs between October and February with a peak in December (horizontal line). Green sea turtles (*Cm*) nest year-round (dashed horizontal line) with a peak around austral winter (June to October; continuous horizontal line).

Diel cycles were also clearly visible in our data (Fig. 4.3). The range of daily temperatures (i.e., the maximum sand temperature - the minimum sand temperature recorded in one day) was generally larger at shallower depth ($F_{1,13} = 3.681$, $p = 0.08$, n = 16 loggers). The mean daily range of sand temperatures was 0.6°C (SD = 0.4°C) at a depth of 30cm, whereas it was 0.2°C (SD = 0.1°C) and 0.3°C (SD = 0.3°C) at depths of 50cm and 70cm, respectively. The range of daily temperatures was also larger in the open habitat (mean = 0.2°C, SD = 0.1°C) compared to the vegetated habitat (mean = 0.5°C, SD = 0.4°C; $F_{1,13} = 3.914$, $p = 0.07$, n = 16 loggers).

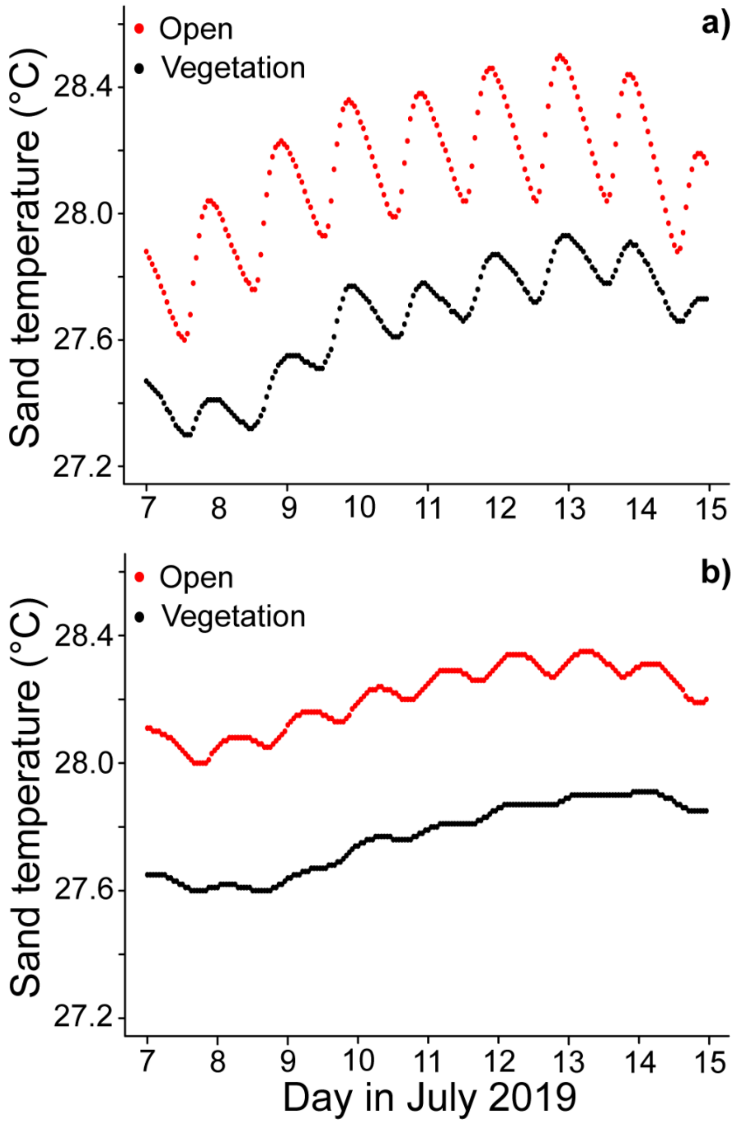

Figure 4.3. Diel variation patterns at two nesting habitats (vegetation and open) on the nesting beach in Diego Garcia, Chagos Archipelago. A point shows raw temperature data on the hour (starting at midnight) between 07/07/2019 and 15/07/2019 from one single logger in each habitat buried at a) 30cm and b) 50cm depth.

Inter-beach and intra-beach thermal variation

Detrended sand temperatures were different between islands of the archipelago (F-value = 282.3, DF = 4, $p < 0.05$), with the highest sand temperatures found on Nelson's Island and the lowest ones found on Petit Ile Coquillage. The difference between sand temperatures found on these two islands was 0.62°C (SE = 0.05°C; Table 4.1). We also recorded different temperatures in the different nesting habitats (i.e., HWL vs open vs shaded; F-value = 1504.0, DF = 2, $p < 0.05$): lowest sand temperatures were recorded at the spring HWL and highest temperatures were recorded in the open, with the mean thermal difference between these two habitats being 0.52°C (SE = 0.02°C; Fig 4.3). Sand temperatures recorded in the vegetation were 0.26°C (SE = 0.02°C) lower than sand temperatures recorded in the open. Lastly, we found a significant but negligible effect of depth in our long-term sand temperature data (F-value = 403.7, DF = 1, $p < 0.05$), with temperatures recorded at a depth of 80cm being 0.08°C (SE = 0.01°C) higher than temperatures recorded at a depth of 30cm.

Sand temperatures recorded with the temperature probe offer further insight into intra-beach thermal variations. Results from this analysis informed on temperature differences between nesting habitats, sites along the beach and depths for ten study days. Similar to the results from the long-term sand temperature records, we recorded different temperatures in different nesting habitats ($\chi^2 = 25.146$, df = 2, $p < 0.01$) with the probe. Lowest temperatures were recorded in the full vegetation. Sand temperatures in the partial vegetation were 0.35°C (SE = 0.08°C) higher. We did not detect any differences between sand temperatures in the open beach and sand temperatures in the full vegetation ($p = 0.57$). As well as thermal differences in nesting habitats, we found thermal differences at different study sites along the beach ($\chi^2 = 48.992$, df = 7, $p < 0.01$) when using the probe. For example, the mean difference between the warmest and the coolest site on Diego Garcia Index Beach was 0.25°C (SE = 0.07°C). On Nelson's Island, thermal differences between sites were more pronounced, with mean sand temperatures at the warmest site being 1.01°C (SE = 0.20°C) higher than temperatures at the coolest site. We did not detect any thermal differences between sites on Egmont ($p = 0.18$). Lastly, we found a significant but negligible effect of depth ($\chi^2 = 4.562$, df = 1, $p = 0.03$) when using the probe, with sand temperatures at a depth of 70cm being 0.01°C (SE = 0.004°C) higher than sand temperatures at a depth of 50cm.

Table 4.1. Sources and extent of thermal variability recorded in the long-term sand temperature and temperature probe data. Sand temperatures were recorded between October 2012 and July 2023 with long-term loggers and ten study dates spread across March and September 2021 and in July and August 2022 with the temperature probe. Values given in column "Extent of thermal variability" are extracted from the output of the statistical models carried out on 1) the mean monthly sand temperature recorded by the long-term loggers or 2) the spot sand temperature readings from the probe. The extent of inter-annual thermal variability is measured as the mean difference between the warmest year and the coolest year in our study. The extent of seasonal thermal variability is measured as the mean difference between the warmest month and the coolest month in a single year. The extent of inter-beach (island) variability is reported as the mean difference between the warmest island and the coolest island. The extent of intra-beach (nesting habitat) variability is reported as the mean difference between the warmest and coolest nesting habitat. The extent of depth variability is reported as the mean difference between the warmest and coolest depth.

Source of thermal variability	**Method**	**Extent of thermal variability**
Inter-annual	*Long-term loggers*	1.03°C (SE = 0.17°C)
Seasonal	*Long-term loggers*	3.00°C (SE = 0.71°C)
Inter-beach: Island	*Long-term loggers*	0.62°C (SE = 0.05°C)
Intra-beach: Site	*Temperature probe*	1.01°C (SE = 0.20°C)
Intra-beach: Nesting habitat	*Long-term loggers*	0.52°C (SE = 0.02°C)
	Temperature probe	0.35°C (SE = 0.08°C)
Depth	*Long-term loggers*	0.08°C (SE = 0.01°C)
	Temperature probe	0.01°C (SE = 0.004°C)

When we only take into consideration temperature probe readings from March 2021 in all nesting habitats, the mean range of temperatures recorded on an individual survey date observed within a specific study site (e.g. DG1) was 1.9°C (SD = 0.7°C; range = 0.8 – 3.0°C; n = 8 sites; Fig. 4.4). The greatest thermal range was found at a site along the Index Beach on Diego Garcia and the site with the smallest thermal range was located on Nelson's Island. Between study sites along a nesting beach, the mean thermal range was 0.53°C (SD = 0.43°C; range = 0.25 - 1.02°C; n = 3 islands), with the largest thermal range observed on Nelson's Island and the smallest observed on Egmont. On the Index Beach on Diego Garcia the thermal range was 0.31°C. When considering both thermal ranges within and across sites along a beach, our empirical observations suggest that the range of sand temperatures available are 3.0°C, 2.6°C, 2.0°C for Diego Garcia, Nelson's Island and Egmont atoll, respectively.

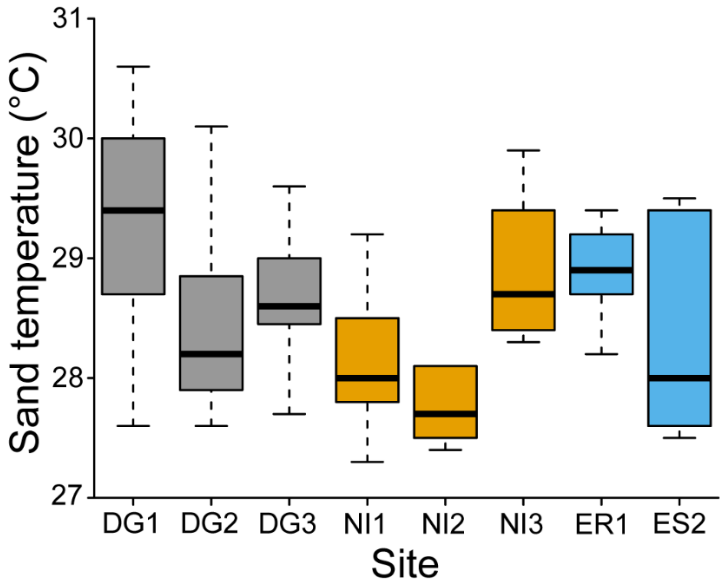

Figure 4.4. Intra-beach sand temperature variation measured using a temperature probe at three sites along nesting beaches on two islands in the Chagos Archipelago: Diego Garcia (DG, in grey), and Nelson's Island (NI, in orange), and one site on Ile des Rats (ER1) and Ile Sudest (ES2) in Egmont atoll (in blue). The data presented here are from March 2021 and at 50cm depth to ensure seasonal variation or depth effects do not bias these results.

DISCUSSION

Recording sand temperatures at sea turtle nesting sites has become a widespread conservation practice (e.g., Matsuzawa et al. 2002; Fuentes et al. 2010; Bentley et al. 2020) given the effect of incubation temperature on embryo survival and hatchling sex ratios (Howard et al. 2014; Santidrián Tomillo and Spotila 2020) ultimately influencing population viability (Hays et al. 2017). Incubation temperature also influences hatchling locomotor performance (Booth 2017). Here we describe one of the longest time series of sand temperatures recorded at a sea turtle nesting site to date, as to our knowledge the previous longest published time series was 6 years (Laloë et al. 2017). We also address a research topic that has previously received little attention, namely thermal variability. Our findings suggest that sand temperatures in the Chagos Archipelago varied inter-annually, seasonally, between beaches, and within beaches, thus providing a wide range of incubation temperatures for turtles nesting in the archipelago. Essentially, our recorded temperatures on nesting beaches in the archipelago all fall within the narrow window of incubation temperatures where successful development of sea turtle embryos occur (i.e., ~27-35°C; Ackerman 1997; Howard et al. 2014).

Previous research showed that Diego Garcia had relatively low sand temperatures during the 2012 and 2013 nesting seasons (Esteban et al. 2016). Our current study extends this finding and shows that low sand temperatures are not anomalous at this site as they were recorded across the five atolls of the archipelago over a decade-long study period (2012-2023). This work also highlights the value of long-term sand temperature studies. Long-term sand temperature studies are critical to understanding inter-annual thermal variation and to capturing outlier years, which may play a significant role in the success of a sea turtle population. For example, a uniquely warm year can lead to female-biased sex ratios (Hays et al. 2021b). In our time series, 2015 was the warmest year, which is likely linked to the ENSO-driven marine heatwave that affected the archipelago in 2015/2016 (Sheppard et al. 2020). In consequence, it is likely that more female hatchlings were produced during the 2015 nesting season on Diego Garcia compared to any other year in the preceding 70-year period (Hays et al. 2021b). On the other hand, a distinctively cold year or heavy rainfall facilitates the production of male hatchlings. Since male turtles can mate with multiple females in a breeding season, a predominantly male cohort produced one year could potentially sustain a population for decades. In contrast to our results, only small inter-annual differences in sand temperatures have previously been reported at other nesting sites (e.g., Hays et al. 1999; Matsuzawa et al. 2002). This may be due to shorter study periods (i.e., one or two nesting seasons), which limits the ability to identify temperature patterns over time as well as outlier years. So, when possible, we recommend long-term data collection, especially since deployment of loggers is relatively inexpensive and logistically uncomplicated (Staines et al. 2022).

Although, the pivotal temperature has not yet been identified for the green or hawksbill turtle populations in the archipelago, our temperature records reveal that sand temperatures straddle 29.0°C, which is broadly representative of the pivotal temperature for TSD for all species of sea turtle (Ackerman 1997; Davenport 1997). 29.0°C was previously used as the pivotal temperature to estimate primary sex ratios in the Chagos Archipelago (Esteban et al. 2016), where it was estimated that the relatively cool temperatures would produce 63% and 53% male hatchlings for green and hawksbill turtles, respectively. Here we report similar sand temperatures as those reported in the 2016 study, suggesting that hatchling sex ratios have been slightly male-biased at this site for the past decade. Although relatively high proportions of male hatchlings have been reported in other parts of the world (e.g. loggerhead turtles at Fethiye beach in Turkey; Kaska et al. 2006), this finding is in stark contrast to many other sea turtle nesting sites around the world where high sand temperatures and female-skewed sex ratios are reported (Hays et al. 2014), such as on Ascension Island (central Atlantic; Godley et al. 2002), St Eustatius (Caribbean; Laloë et al. 2016), and Raine Island (Australia; Booth et al. 2020). In this sense, the Chagos Archipelago is a relatively unusual sea turtle rookery and likely one that will be resilient to warming sand temperatures predicted to occur with climate change (Esteban et al. 2016). Although, sea level rise driven by climate warming is a concern for the Chagos Archipelago as a low-lying atoll (Rivas et al. 2023). Recently, Mortimer et al. (2020) highlighted the importance of the Chagos Archipelago to nesting turtles both regionally and globally. The review of nest numbers in the south-west Indian Ocean revealed that the Chagos Archipelago hosts 39-51% of hawksbill nests and 14-20% of green turtle reproduction for that region. In addition, nesting has increased 2-5 times for hawksbill turtles and 4-9 times for green turtles since 1996, with the most recent estimates of 6,300 and 20,500 clutches laid annually, for hawksbill and green turtles, respectively (between 2011-2018; Mortimer et al. 2020). The size of the nesting populations add weight to the importance of our findings, since these populations that are very important regionally are likely to be resilient to sand warming.

Seasonal thermal variation was highlighted as an important driver of sand temperatures in some of the first studies reporting sea turtle sex ratios (Mrosovsky et al. 1984, 1994). In South Carolina and Georgia, seasonal changes were found to have a considerable effect on loggerhead (*Caretta caretta)* hatchling sex ratios, where clutches laid during the coolest period of the nesting season produced no females, and clutches laid in the warmer period produced 80% females (Mrosovsky et al. 1984). Likewise, in Suriname a peak in male green turtle hatchlings was observed corresponding to the coolest period of the nesting season (Mrosovsky et al. 1994). Seasonality had the most influence on thermal variability in our study, modulating sand temperatures by up to 3.0°C over a year. Since green sea turtles nest year-round in the Chagos Archipelago (Mortimer et al. 2020), the nesting period spans across this wide variation in sand temperatures. In addition, peak nesting season is between June to September (Mortimer et al. 2020), which spans the austral winter. Taken together, this suggests that 1) different sex ratios are produced throughout the nesting season, as seen in previous studies, and 2) over one nesting season it is likely that balanced, or slightly male-biased sex ratios are produced across the archipelago. On the other hand, the hawksbill turtle peak nesting window falls between October and February (Mortimer et al. 2020), which is during the austral summer when sand temperatures are at their highest, so hatchling sex ratios may not be as male-biased for this species.

Our results revealed inter-beach thermal variation on different islands across the Chagos Archipelago, with the warmest beach being on average 0.62°C warmer than the coolest beach. While we did not record variables that might explain these thermal differences, at other sites sand albedo is known to be a driver of inter-beach thermal variation. On Ascension Island, a 4°C variation in sand temperature between 12 nesting beaches was strongly linked to beach albedo, with darker sand beaches being much warmer than light-coloured beaches (Hays et al. 1995, 1999). Similarly, in Cape Verde, sand temperatures recorded on dark-coloured beaches were 1.8°C warmer than sand temperatures on light-coloured beaches (Laloë et al. 2014). Furthermore, abiotic factors that are known to influence sand temperatures at sea turtle nesting sites include sand grain size, sand water content, and sand conductivity (Speakman et al. 1998). So, there is a wide range of variables that can influence sand temperatures at a site, leading to different beaches presenting different thermal environments. It is therefore recommended to record sand temperatures at different beaches within a nesting site to provide a more holistic view of temperatures experienced at a site. This is particularly relevant in the Chagos Archipelago where nests are scattered across some 55 islands (Mortimer et al. 2020), and individuals are known to migrate from one nesting beach to another during a single nesting season (personal observation), which has also been observed in the Caribbean (Esteban et al. 2015).

Our study also shows the importance of intra-beach thermal variation at our study site, and how different nesting habitats expose clutches to different thermal conditions. The islands of the Chagos Archipelago are densely vegetated, and vegetation assemblages differ along a single nesting beach, such that on Diego Garcia one section of the nesting beach is heavily vegetated with high canopy *Cocos nucifera* and another section with dense shrub *Scaevola* (Esteban et al. 2016). Although nests on Diego Garcia are predominantly in the vegetation, turtles also nest in the open where there is little shade (Stokes et al. 2024). Interestingly, we also recorded low sand temperatures in the open nesting habitat. This is possibly due to the cooling effect of over wash from spring tides or to the presence of a high table. Water tables on low-lying islands are known to be dynamic, rising and falling with the tide, and raised during prolonged periods of heavy rainfall (Bailie et al. 2021). However, it is important to note that clutches laid too close to the high water line may be exposed to increased flooding, which can cause reduced hatching success (Martins et al. 2022b).

Like other studies around the world, our findings highlight the importance of natural shading on sea turtle nesting beaches (Reboul et al. 2021). Preserving native vegetation and planting appropriate vegetation at the back of a nesting beach could be one of the most effective strategies to mitigate future warming sand temperatures (Kamel 2013). However, despite the cooling benefits, negative effects could occur, such as root growth into nests (Conrad et al. 2011), and so careful considerations must be taken. For warm nesting grounds with no natural vegetation, management strategies can be put in place to lower sand temperatures, such as nest irrigation (Smith et al. 2021; Gatto et al. 2023), nest relocation (Esteban et al. 2018) or artificial shading (Reboul et al. 2021; Wiggins et al. 2023).

Our finding suggests that warming of the sand as part of climate change is unlikely to be a pressing concern in the Chagos Archipelago. Triaging threats to sea turtles is an important part of conservation planning (Fuentes et al. 2023) and in this regard it might be that sea level rise and the resulting habitat loss and nest inundation from coastal squeeze (Mazaris et al. 2009) is more of a threat in the region than warming sand temperatures. Islands in the Chagos Archipelago are low lying atolls and hence, in common with atolls around the world, at threat from sea level rise (Bellard et al. 2013; Wu et al. 2021). Indeed, sea level rise is already driving threat mitigation measures in some parts of the world. For example, at Raine Island (northern Great Barrier Reef, Australia), sea water inundation of nests had led to programme of importing sand to build up the nesting beaches (Hamann et al. 2022; Smithers and Dawson 2023). Assessing this threat of inundation, and designing mitigation measures, is therefore an important conservation concern not only for the Chagos Archipelago but all other low-lying atolls around the world (Ware and Fuentes 2018; Gammon et al. 2023).

Lastly, we found a minimal effect of nest depth on sand temperature across the range of depths considered. Previous studies around the world have also shown that nest depth has minimal influence on sand temperatures at nesting beaches (Carr and Hirth 1962; Hays et al. 1999; Esteban et al. 2016). However, some studies on smaller sea turtles such as loggerheads (*Caretta caretta*) have shown that shallower nests display larger within-nest thermal variation compared to deeper nests (Houghton and

Hays 2001). It has been suggested that sea turtles might be able to select different thermal microhabitats by laying their clutches at different depths in the sand (Marco et al. 2018). Such a strategy would help turtles adapt to varying sand temperatures, but unfortunately our study offers little evidence to support this hypothesis.

CONCLUSION

In conclusion, our study identifies different levels of sand temperature variability at a key sea turtle nesting site. We demonstrate how thermal variability can be captured using a handful of loggers strategically placed in the different turtle nesting habitats. Our results underline the need to consider thermal variability both temporally and spatially to capture the range of temperatures experienced at a beach. Furthermore, our work highlights the need to take potential sources of thermal variation into account when modelling sea turtle population dynamics such as sex ratios. Given the risks of increasing sand temperatures on population viability, the continued long-term monitoring of sand temperatures at sea turtle nesting sites is recommended, especially since temperature loggers are a relatively cheap and highly informative conservation tool.

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CHAPTER FIVE: Predation of sea turtle eggs by rats and crabs

This chapter was amended from published work:

Stokes HJ, Esteban N, Hays GC (2023) Predation of sea turtle eggs by rats and crabs. Mar Biol 171:17. https://doi.org/10.1007/s00227-023-04327-9

Disclaimer: GCH, NE and HJS conceived the study. HJS and NE conducted the fieldwork. HJS and GCH led the data analysis and writing with contributions from all authors.

ABSTRACT

Egg predation by invasive and native species may have severe impacts on endangered species and negatively affect species recovery. We assessed the levels of egg predation within green turtle (*Chelonia mydas*) clutches on the island of Diego Garcia (7.42°S, 72.45°E), Chagos Archipelago (Indian Ocean). Native coconut crabs (*Birgus latro*) and ghost crabs (*Ocypode spp.*), as well as introduced black rats (*Rattus rattus*), were predators of eggs, with these species entering nests via tunnels dug obliquely in the sand. Often whole eggs were removed from clutches. For example, the mean clutch size at oviposition (mean 127.8 eggs, n = 23, range = 74 - 176) was significantly larger than at the end of incubation (mean 110.9 hatched and unhatched eggs, n = 16, range = 9 - 147). In other cases, egg predation was recorded where the egg had been opened and contents were eaten in the nest. Overall, hatchling success (the percentage of eggs laid leading to a hatchling emerging from the egg) was 64.9%, while 3.1% of eggs were eaten within nests, 18.1% died during incubation without predation and 13.9% were removed. We reviewed evidence from 34 sites around the world identifying 36 predators that were either native (e.g., crabs, and goannas, n = 30) or invasive (e.g., rats, and pigs, n = 8). Depending on location a predator could be identified as both native and invasive (e.g., dogs). We discuss how either nest protection and/or invasive predator eradication may be used to increase egg survival and when these approaches might be used.

KEYWORDS

invasive species, predator management, conservation, rat eradication, marine protected area (MPA), marine turtle

INTRODUCTION

The survival rate of offspring is a key demographic factor that drives the success of populations and hence assessment of factors driving offspring survival has been a central component of ecological studies for many decades (Gibson et al. 2017; Reglero et al. 2018). In the most general terms, there is trade-off between parental investment in individual offspring and their survival. For example, some fish that produce millions of small eggs that will tend to have lower rates of survival (Anderson and Gillooly 2021), while some large vertebrates, like whales and elephants, produce a few large offspring and have extended parental care resulting in higher offspring survival (Lueders et al. 2012). Due to the key role in driving population dynamics, factors that cause long-term changes in offspring survival rates may influence population trajectories (Reichert et al. 2020; Parker et al. 2021). As well as levels of mortality driven by natural predators, other factors that may increase offspring mortality include introduced invasive predators (Spencer 2002), direct human harvesting, including poaching of eggs (Pheasey et al. 2021) and climate warming (Hao et al. 2021).

Sea turtles are a group where several species are endangered, particularly at regional scales, and where many of these disparate factors can play important roles in influencing offspring survival and hence population trajectories (Mazaris et al. 2017). Female sea turtles typically produce several clutches in a single nesting season laying several hundred eggs (e.g. Hays and Speakman 1991). In some parts of the world, there may be high levels of nest predation from natural occurring predators. For example, in Florida, raccoons (*Procyon lotor*) are an important nest predator and have led to efforts of protecting nest sites with metal cages (Engeman et al. 2016) or removal of raccoons from islands as an effective management strategy (Garmestani and Percival 2005), while in Australia, yellow-spotted goannas (*Varanus panoptes*) are important nest predators (Lei and Booth 2017b). Red foxes (*Vulpes vulpes*) are a widely recorded nest predator in the Mediterranean leading to screening of nests with metal grids in Turkey (Kaska 2000; Kaska et al. 2010). In some areas, particularly historically but also more recently, harvesting of eggs has been thought to underpin declines in population abundance (Cáceres-Farias et al. 2022). As embryo mortality increases in sea turtle nests at high nest temperatures, there is also concern that embryo mortality rates will increase associated with climate warming (Laloë et al. 2017; Hays et al. 2017).

Conversely, major increases in nesting numbers in some parts of the world have often been attributed to conservation efforts reducing the level of egg poaching (Mazaris et al. 2017).

Given the importance of hatchling survival for sea turtles, we assessed the relative importance of nest predation for green turtles (*Chelonia mydas*) nesting at a major rookery on an isolated island where harvesting or poaching of eggs is zero but where there are a range of potential predators, both natural and introduced. In this way our work helps identify the importance of managing and / or removing invasive predators that may have several negative ecosystem consequences.

MATERIALS AND METHODS

The study was undertaken on the island of Diego Garcia (7.42°S, 72.45°E), Chagos Archipelago (Indian Ocean) which lies in the centre of one of the world's largest marine protected areas (MPA; Hays et al. (2020)). After two centuries of exploitation, turtles in the Chagos Archipelago have been protected since around 1970 with all life history stages (nests, foraging juveniles, nesting adults) receiving full protection. Diego Garcia is the only inhabited island in the archipelago.

We patrolled the index beach on Diego Garcia (Fig. 5.1a) at night in search of nesting females and early morning for tracks leading to successful nests or a nesting female. If possible, we counted eggs within clutches as they were laid but if this was not possible (e.g., due to the turtle covering the nest with her rear flippers) then the nest was carefully excavated immediately after the turtle disguised her nest and the eggs were counted and carefully placed back in the same general order as they were laid. Nests were marked via triangulation to tree trunks or branches of nearby vegetation that were marked with different coloured tape. The distance from each tree/branch to the nest was recorded along with the tape colour and a bearing was taken from each tree to the nest.

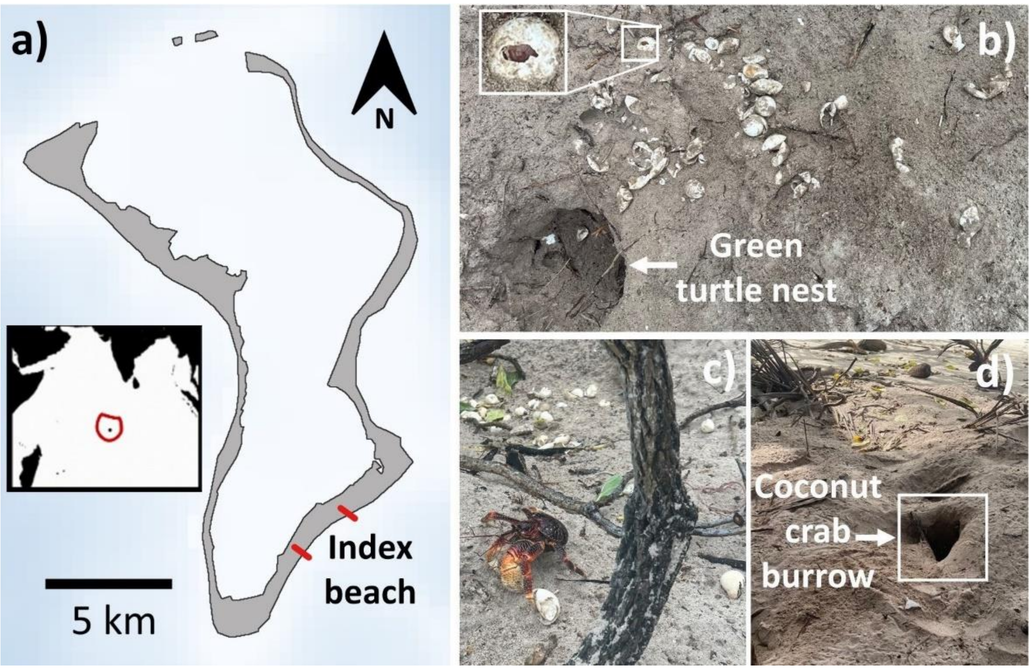

Figure 5.1. a) Diego Garcia (land shaded grey) and the index beach (indicated by the red lines; 2.8 km) with a map showing the location of the Chagos Archipelago in relation to the wider Indian Ocean (red boundary = marine protected area). **b)** Remnants of a green turtle nest predated by a coconut crab (*Birgus latro*) with scattered eggshells on the sand surface and pierced eggs with egg remains. **c)** A coconut crab piercing and eating a green turtle egg. Predated scattered eggs can be seen in the background on the sand surface. **d)** Coconut crab burrow into a green turtle nest which was used by other predators (e.g., black rats (*Rattus rattus*), ghost crabs (*Ocypode spp*.), strawberry hermit crabs (*Coenobita perlatus*), warrior crab (*Cardisoma carnifex*) to scavenge eggs.

Nests were monitored for signs of hatching after 60 days of incubation. Nests were excavated at least 65 days after clutch deposition. For each excavation, hatch success was recorded through counts of empty eggshells and unhatched eggs. Unhatched eggs were opened to determine the stage at which development had stopped, using descriptions and diagrams from Smith et al. (2021). The number of predated eggs (eggs with small, snipped hole / slit; ~1.5cm) indicative of being opened by crabs (Maros et al. 2003) were recorded (Fig. 5.1b-d). Nests were also excavated after observing hatching events from nests where the clutch size was not counted at oviposition. Nest depth was measured to the top and bottom of the egg chamber.

Nests (marked and un-marked) were checked for signs of predation, to note the predator and incident (e.g., type and number of predators around the nest, location of burrow or access point, and the number of opened eggs if seen on the surface).

Global review

We compiled literature studies that identified predators of sea turtle nests around the world. To do this we searched WoK using the search terms under TOPIC ("sea turtle*" AND "nest predat*"), ("sea turtle*" AND "egg predat*"), ("marine turtle*" AND "nest predat*") and ("marine turtle*" AND "egg predat*") and then completed a backward citation search from the most recent paper (Espinoza-Rodríguez et al. 2023). Only dominant primary and secondary predators were included in the global review. Other predators reported in studies but were stated to cause little impact are listed in the results section but are not included in the global predator map.

RESULTS

Field observations

Although not observed for nests where oviposition and excavation counts were conducted, there were observations of predators in nests that we had come across during other data collection along the index beach. We observed ghost crabs (*Ocypode spp*.), coconut crabs or robber crabs (*Birgus latro*) and black rats (*Rattus rattus*) consuming turtle eggs at the sand surface (Fig. 5.1b; Fig. 5.1c; Fig. 5.1d). In all these cases where we observed eggs being eaten, the adjacent nest had at least one tunnel running obliquely down towards the nest chamber. On many separate occasions of opportunistic observations of unmonitored nests, we observed recently laid clutches (in the last week or so) with eggs removed from the nest and eaten on the sand surface. Between 05/02/2021 – 31/03/2021 counts of eggs on surface close to fresh burrows ranged from 2 to 69 eggs (mean ± SD: 14.8 ± 16.1 eggs, n = 25; Fig 4.1b; Fig 4.1c, Table S5.2). Coconut crabs dig large burrows (Fig. 5.1d) into the nests and the eggs are usually brought to the surface where evidence lies in scattered eggshells on the sand. These large burrows present an opportunity for rats, ghost crabs, strawberry hermit crabs (*Coenobita perlatus*), that were observed utilising the burrow and scavenging eggs. Hermit crabs, smaller ghost crabs, warrior crabs (e.g., *Cardisoma* *carnifex*) and fiddler crabs (*Uca spp*.) were observed to loiter around predated nests and feed on dried eggshells presumably left by coconut crabs. Rats were also observed digging down into the sand. From observations on Diego Garcia, it seems coconut crabs cause the most impact to nest success, with one individual able to decimate a nest by removing a large proportion of eggs, along with creating an opportunity for other predators to enter the nest easily.

Clutch size

Nests were excavated between 66-76 days after eggs were laid (mean ± SD = 73 ± 3 days, n = 19). The clutch size, measured at oviposition, ranged from 74 to 179 eggs (mean ± SD = 127.8 ± 27.4 eggs, n = 23). Clutch size increased in larger turtles, with the CCL explaining 42% of the variance in the number of eggs per clutch (Fig. 5.2a, $F_{1,21}$ = 15.1, r^2 = 0.42. $P < 0.001$). The number of hatched and unhatched eggs remaining in the nest at the end of incubation ranged from 9 to 147 eggs (mean ± SD = 110.9 ± 40.3 eggs, n = 16), i.e., 13.2% lower than the mean number at oviposition. Where both the number of eggs at oviposition and at excavation was measured for the same clutch, the number at excavation was similarly 13.9% lower, a difference that was significant (means 133.1 and 114.6 eggs respectively, paired *t* test, t_{12} = 2.61, P = 0.023). In some cases, the difference in number of eggs at oviposition and at excavation was extreme. For example, one clutch had 74 eggs at oviposition but only 9 at excavation, while for another the numbers were 140 and 81 respectively (Fig. 5.2b; Fig. 5.2c; Table S5.1). In no cases were entire clutches dug up.

The number of hatchlings emerging from nests was mean ± SD = 85.4 ± 46.4 (n = 16 clutches). For clutches where both the number of eggs at oviposition and the number of hatchling emerging were assessed, the mean ± SD hatching success (% of eggs laid that led to hatchling emerging from the egg) was 64.9 ± 38.5% (n = 13 clutches). The mean number of eggs per clutch with holes indicative of crab predation within the nest was 4.1 eggs, i.e., 3.1% of the mean number of eggs at oviposition, and the mean number of eggs that failed to complete development but were not predated was mean ± SD = 24.2 ± 34.2 eggs per clutch (n = 13), i.e., 18.2% of the mean number of eggs at oviposition. Nest depth to the top of chamber was mean ± SD = 52 ± 12 cm (n = 13) and to the bottom of the chamber was mean ± SD = 66 ± 14 cm (n = 13). Crabs excavated between 1 - 3 burrows angled at around 45° to reach the top of the egg chamber.

In summary, when assessing the fate of eggs within a clutch about 13.9% of eggs were removed, 3.1% were eaten and left inside the nest, 18.1% failed to complete development (not predated) and 64.9% emerged as hatchlings.

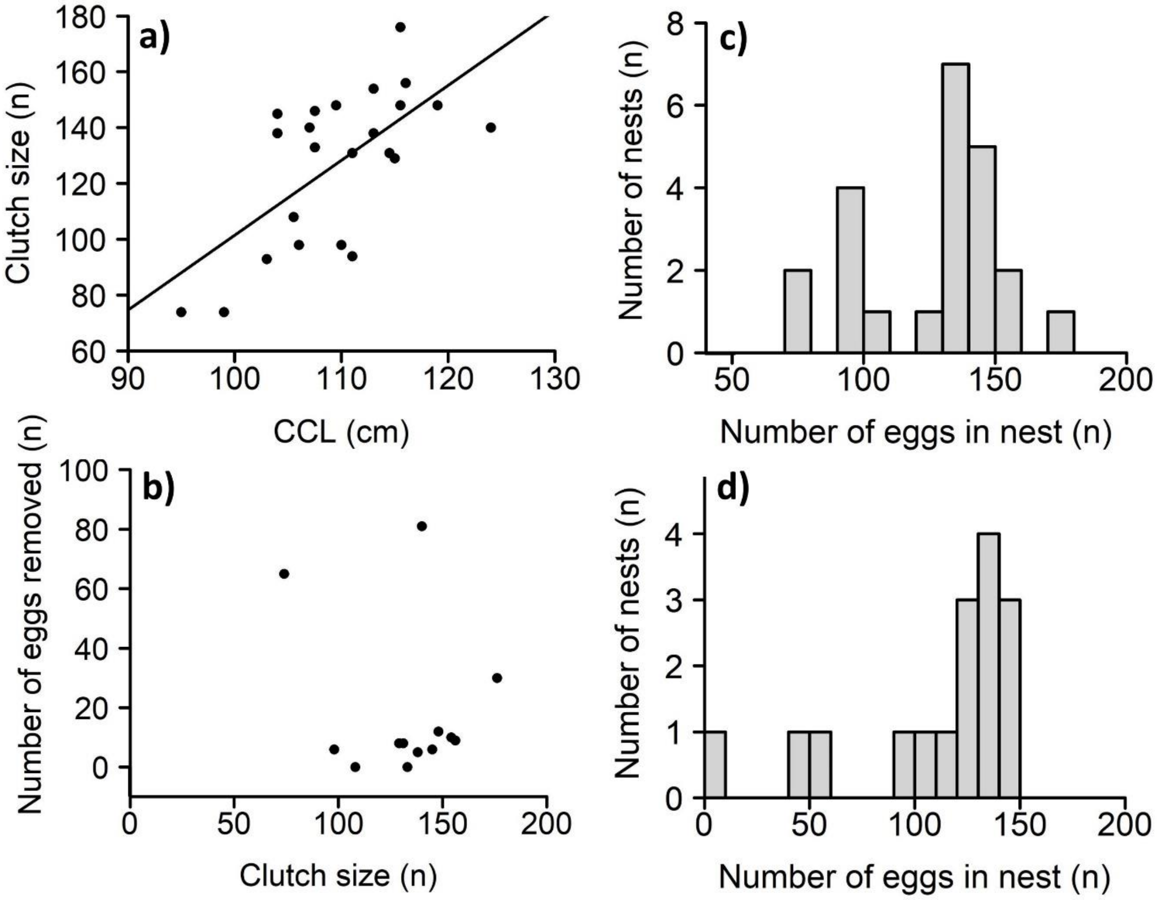

Figure 5.2. For green turtles on Diego Garcia, Chagos Archipelago, we show the **a)** relationship between the curved carapace length (CCL) and clutch size ($F_{1,21}$ = 15.1, r^2 = 0.42, $P < 0.001$). **b)** number of eggs removed from the nest between oviposition and excavation in relation to clutch size ($F_{1,11}$ = 0.41, r^2 = 0.04, P = 0.5) and the distribution of the number of eggs at **c)** oviposition and **d)** excavation (Table S5.1).

Predators of sea turtle nests around the world

From 40 studies (including our current study), we found a range of both vertebrate and invertebrate predators of sea turtle nests around the world as well as native and invasive species (Fig. 5.3; Table S5.3). We found predation studies at 34 sites for all sea turtle species, including green, loggerhead (*Caretta caretta*); olive ridley (*Lepidochelys olivacea*), hawksbill (*Eretmochelys imbricata*), flatback (*Natator depressus*), leatherback (*Dermochelys coriacea*) and Kemp's ridley (*Lepidochelys kempii*) turtles. Thirty-six predator species were identified, eight of which were identified as invasive, including feral pigs, *Sus scrofa* (Pereira et al. 2023); red foxes (Lei and Booth 2017b); armadillo, *Dasypus novemcinctus* (Engeman et al. 2006); Asian mongoose *Herpestes javanicus* (Leighton et al. 2011) and rats (present study). Depending on the site location a predator could be classed as invasive or native (e.g., dogs and coyotes). From our global review, we found the most important predators are medium sized mammals (e.g., pigs, red foxes), crabs (e.g., yellow crab, *Johngarthia lagostoma*) and *Varanus spp*. Some of the species we have included (in Fig. 5.3) are classed as secondary or opportunistic predators but are still known to cause damage to nests (e.g., rats, and vultures). Other predators were found in our search but were recorded as having little impact on nests at the study site (and excluded from Fig. 5.3) include, striped skunk (*Mephitis mephitis*), Tayra (*Eira barbara*), opossum (*Didelphis spp.*), caracara (*Caracara cheriway*) and maggots (Espinoza-Rodríguez et al. 2023), spotted skunk (*Spilogale putorius*), and bobcats (*Felis rufus;* Engeman et al. 2006), Northern river otter (*Lontra canadensis*), American mink (*Mustela vison*), crow (*Corvus spp.*), snakes (Butler et al. 2020).

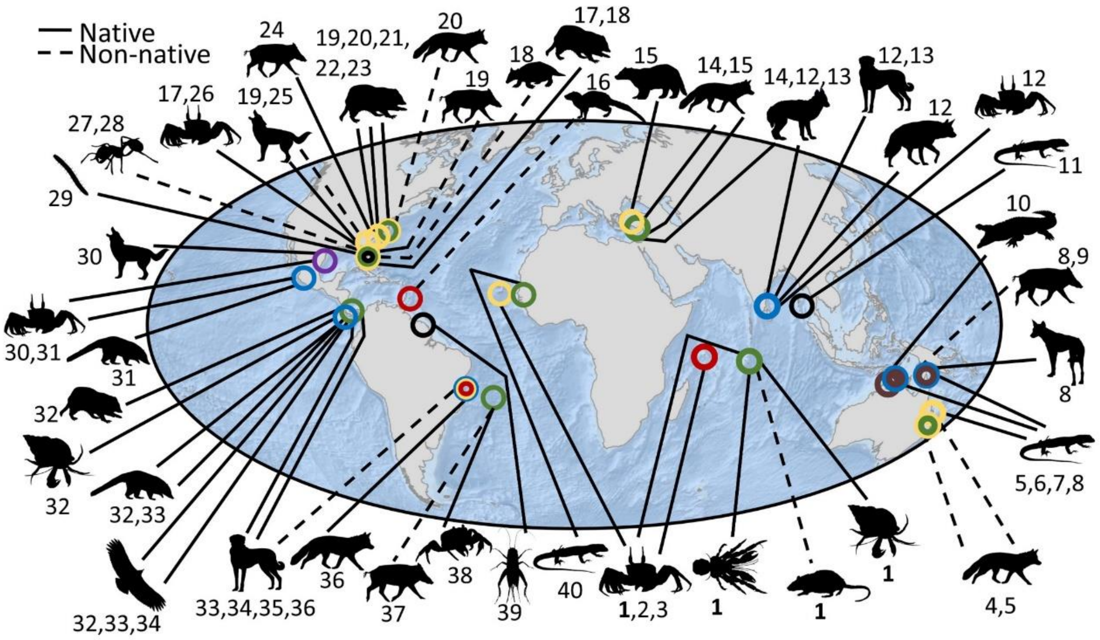

Figure 5.3. Examples of common sea turtle nest predators identified across the world (Table S5.3) shown by icons including mammals (e.g., canids, procyonids, pigs, mongoose, armadillo), reptiles (goannas, saltwater crocodiles), invertebrates (e.g., ghost crabs, coconut crabs, ants, mole crickets). Secondary and opportunistic predators of accessible nests are also included, such as rats, birds (e.g., vultures), and hermit crabs. 1 = coconut crab, ghost crab, rat, hermit crab (present study); 2 = ghost crab (Marco et al. 2015); 3 = ghost crab (Hitchins et al. 2004b); 4 = red fox (O'Connor et al. 2017); 5 = red fox, goanna (Lei and Booth 2017b); 6 = goanna (Lei et al. 2017); 7 = goanna (Lei and Booth 2017a); 8 = goanna, feral pig, dingo (Nordberg et al. 2019); 9 = feral pig (Whytlaw et al. 2013); 10 = saltwater crocodile (Whiting and Whiting 2011); 11 = Asian water monitor (Sivasundar and Devi Prasad 1996); 12 = ghost crab, hyena, feral dog, jackal (Tripathy and Rajasekhar 2009); 13 = domestic dog, golden jackal (Bhupathy 2003); 14 = red fox, golden jackal (Brown and Macdonald 1995); 15 = red fox, badger (Başkale and Kaska 2005); 16 = Asian mongoose (Leighton et al. 2011); 17 = raccoon, ghost crab (Brost et al. 2015); 18 = raccoon, armadillo (Engeman et al. 2006); 19 = feral pig, coyote (Butler et al. 2020); 20 = red fox, raccoon (Halls et al. 2018); 21 = raccoon (Welicky et al. 2012); 22 = raccoon (Engeman et al. 2010); 23 = raccoon (Ratnaswamy et al. 1997); 24 = feral pig (Engeman et al. 2019); 25 = coyote (Lamarre-DeJesus and Griffin 2015); 26 = ghost crab (Bouchard and Bjorndal 2000); 27 = red fire ant (Parris et al. 2002); 28 = red fire ant, tropical fire ant, little fire ant (Wetterer et al. 2014); 29 =

click beetle larvae (Donlan et al. 2004); 30 = coyote, ghost crab (Shaver 2020); 31 = raccoon (Garcıía et al. 2003); 32 = raccoon, hermit crab, coati, vulture (Espinoza-Rodríguez et al. 2023); 33 = coati, vulture, dog (Fowler 1979); 34 = vulture, dog (Burger and Gochfeld 2014); 35 = dog (Siqueira-Silva et al. 2020); 36 = domestic dog, fox (Nayelli Rangel Aguilar et al. 2022); 37 = pig (Pereira et al. 2023); 38 = yellow crab (de Faria et al. 2022); 39 = mole cricket (Maros et al. 2003); 40 = Nile monitor (Sampaio et al. 2022). Symbol colour: green = green turtle (*Chelonia mydas*); yellow = loggerhead (*Caretta caretta*); blue = olive ridley (*Lepidochelys olivacea*); red = hawksbill (*Eretmochelys imbricata*); brown = flatback (*Natator depressus*); black = leatherback (*Dermochelys coriacea*); purple = Kemp's ridley (*Lepidochelys kempii*). Non-native = imported, invasive or introduced. Icon source: R package Rphylopic (Gearty et al. 2023).

DISCUSSION

Predators impact sea turtle clutches in a number of ways. In some parts of the world entire clutches can be dug up and predated. For example, in Australia, dingoes (*Canis lupus dingo*), goannas, and feral pigs can cause complete loss of flatback and olive ridley nests through nest excavation and consumption or damage to every egg in a clutch (Nordberg et al. 2019). However, this type of nest excavation and entire nest destruction was not observed on Diego Garcia, but instead it appeared as if eggs were being removed individually by crabs and rats entering the nests via tunnels. We report both coconut crabs and ghost crabs predating eggs and to the best of our knowledge we report the first observations of coconut crabs actively burrowing into sea turtle nests to feed upon eggs. Coconut crabs play a critical ecological role in Indo-Pacific Island ecosystems. As omnivores, they feed on an array of plants and animals and their scavenging activity aids decomposition of rotting material (Stensmyr et al. 2005). Through active hunting, coconut crabs act as a top predator on island ecosystems and have been referred to as the 'ruler of the atoll', even sometimes killing birds (Laidre 2017). Our observations suggest that the impact of direct egg predation by coconut crabs is magnified by their tunnelling into nests, thereby creating a pathway for other predators. Similarly, in Australia, Lei and Booth (2018) found that the opening of a nest by a goanna caused a significant increase in visitation rates to the nest by other goannas and crabs. On high density sea turtle nesting beaches, clutches are dug up by subsequent nesting turtles and causes a significant loss of eggs directly and provides an opportunity for other predators to find eggs (Ocana et al. 2012).

Our findings add to the growing evidence that crabs can be important predators of sea turtle nests. For example, Marco et al. (2015) reported that in unprotected loggerhead turtle nests on Cape Verde (Atlantic Ocean), on average ghost crabs (*Ocypode cursor*) predated 50% of the eggs. Furthermore, Marco et al. (2015) suggested that dominant crabs might defend the nest they prey upon, sequentially removing eggs over a period of time. On Trindade Island in Brazil, de Faria et al. (2022) observed yellow crabs predating eggs as they were laid by green turtles and report an average loss of three eggs per nest during the nesting stage. Similarly, ghost crabs have been reported predating high numbers of turtle eggs in other parts of the world (e.g. >15% of eggs in the Seychelles (Hitchins et al. 2004b). In other areas, crab predation is lower. For example, for green turtles in Malaysia, just 1.3% of eggs were lost due to ghost crab predation (Ali and Ibrahim 2002). The drivers of this variable effect from ghost crabs are unknown but may be linked to crab density or the ability of crabs to access clutches is linked to nest depth. Certainly, on Diego Garcia it appears that tunnels dug by coconut crabs is a route of access to eggs for ghost crabs, allowing them to access deeply buried eggs that might otherwise be unavailable. On some nesting beaches, crab predation is frequent on hatchlings crawling from the nest to the sea which can cause a significant decrease in hatchling recruitment (Martins et al. 2021).

Across the world, rats introduced to islands have had huge negative ecosystem impacts such as declines in seabird numbers (Lock 2006; Caut et al. 2008; Carr et al. 2013). These seabird declines in turn can impact ecosystem functioning such as loss of nutrients, from bird guano, decreasing coral reef ecosystem productivity and diversity (Graham et al. 2018) even resulting in a change in coral reef fish behaviour (Gunn et al. 2023). Rats also impact sea turtles. For example, in New Caledonia invasive rats heavily feed upon seabird eggs and chicks, however, in the absence of birds outside of their nesting season, rats shift their diet and prey on green turtle hatchlings (Caut et al. 2008). Although, rat predation of hatchlings has been reported, to our knowledge our study is the first to report observations of rat predation on sea turtle eggs, likely facilitated by nest access through the burrows created by coconut crabs.

While our study was not able to resolve the relative importance of crab versus rat predation, we were able to show that together these predators were influencing nest success, predating almost 15% of eggs. Addressing the relative importance of these different predators might potentially be addressed using modern camera technology. For example, Lei and Booth (2017b) elegantly used cameras to identify predators of turtle nests in Australia.

There are essentially two methods to reduce predation of sea turtle eggs: protection of nests or eradication of the predator. Predator eradication is certainly an option where predators are an introduced species. For example, introduced feral pigs historically decimated green turtle nests on Trindade Island, Brazil and pig removal has led to recovery of nesting numbers (Pereira et al. 2023). Similarly, on Keewaydin Island, Florida, pig eradication resulted in a decrease from 87% to just 1% of nests destroyed by this invasive predator (Engeman et al. 2019). In some cases, eradication of invasive species may have very broad ecosystem benefits. For example, ongoing efforts to remove rats from oceanic islands, including within the Chagos Archipelago (Russell and Holmes 2015; Benkwitt et al. 2021) is designed primarily to benefit sea birds and also improve the quality of neighbouring reefs, but may have the additional benefit of reducing predation on turtle eggs (our study).

Our global analysis revealed that predation of sea turtle eggs is more often than not by native animals, such a raccoons and crabs. In cases of high predation by native animals, then protection of nests, for example with cages, may help reduce predation both with clutches relocated to hatcheries as well as those protected *in situ* (Marco et al. 2015). For example, in Georgia, large mesh screens are designed to protect nests from raccoons and secondary smaller mesh screens to protect against ghost crabs (Butler et al. 2020). In Guinea-Bissau, Sampaio et al. (2022), used a variety of techniques to protect green turtle nests from Nile monitors (*Varanus niloticus*), including scent covering, by sprinkling clove essence aqueous solution on the surface sand to mask the scent of turtle eggs, track covering to remove visual cues and square metal nets (over and buried into the sand). However, such intervention should be conducted with measures to ensure Nile monitors were not detrimentally affected in the process of protecting sea turtle eggs. In some cases, however, protection via fences has not been sufficient, for example, in Java, Indonesia, all fenced and unfenced natural nests were eaten by monitor lizards (Maulany 2013). Such approaches to protect sea turtle nests from native predators may be costly and difficult to implement and so it may be important to assess if such predation is having an important negative impact on a population’s trajectory, before deciding if intervention is warranted. For example, both at Diego Garcia and in the Cape Verde Islands, with 17% and 50% predation by crabs respectively, nesting numbers are increasing (Mortimer et al. 2020; Hays et al. 2022a), suggesting that crab predation is not sufficient to prevent population increases.

Often in sea turtle research, clutch size is estimated by excavating nests once hatchlings have emerged and then by counting shell fragments and unhatched eggs. We echo the concerns of Marco et al. (2015) that such clutch size estimates may be compromised at sites where eggs are being removed from clutches by crabs. In those cases, obviously the clutch size will be underestimated, sometimes vastly, at nest excavation. In an extreme case we found that only nine eggs remained in the nest chamber at the end of incubation while Marco et al. (2015) reported that 100% of eggs could sometimes be removed from clutches by crabs. In common with many studies, we found that larger females (with a resulting larger body cavity) had a higher reproductive effort and tended to lay more eggs per clutch (van Buskirk and Crowder 1994). The most parsimonious explanation for why clutch size increases with female size is that females are minimising the energetic cost of nesting per egg laid (Hays and Speakman 1991). In other words, laying many more and smaller clutches would be much more energetically expensive compared to a few large clutches. It might be argued that larger clutches might be more susceptible to being located and hence eaten, if they have a larger odour signature. However, we found no relationship between clutch size and the number of eggs removed, suggesting that clutches were located by predators regardless of their size.

In summary, we identified predation of sea turtle nests by crabs and rats but, while levels of predation could sometimes be very high for individual nests, nest predation does not seem to be preventing an increase in nesting numbers. Presumably the impacts of nest predation on Diego Garcia are offset by the complete protection nests receive from any human harvesting.

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CHAPTER SIX: Camera trapping: A novel approach to assess population estimates of nesting sea turtles

This work is a manuscript in preparation for Methods Ecol Evol as:

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Disclaimer: NE and GCH conceived the study. HJS and NE completed the fieldwork. HJS compiled and analysed images. HJS, GCH and NE conducted statistical analyses. HJS led the writing of the manuscript with contributions from all authors.

ABSTRACT

Population estimates are difficult to obtain for animal groups that are elusive or rare. For sea turtles, estimates are often calculated from track and nest counts, yet this is difficult at remote beaches. Here we investigate the applicability of camera traps at nesting beaches. Thirteen camera traps were deployed on a nesting beach at Diego Garcia, Chagos Archipelago to capture images every 30 min between 07:00-08:30 hr daily between 2021-2022. Foot patrol surveys were conducted across April-May 2021 and August 2022 (14, 13, and 21 survey days, respectively). From foot patrols we observed an increase in tracks around neap tides (mean = 6.4; SD = 4.5; n = 165 tracks) compared to spring tides (mean = 3.5; SD = 3.30; n = 74 tracks). Camera traps can be used to estimate track longevity which was also higher during neap tides (mean = 4.1; SD = 2.2 days; n = 41 tracks) compared to spring tides (mean = 3.1; SD = 2.2 days; n = 33 tracks). Camera traps and foot patrols estimated a mean daily track count of 5.3 and 6.4 over 50 days (neap tides), respectively. Using simulated data, sampling variation for the estimated mean number of tracks per day decreased as beach coverage increased. Camera traps could act as a complimentary tool to fill in gaps about emergence activity and abundance estimates at sites that would otherwise have little to no assessments. Furthermore, they can be used to assess variations in nesting seasons as a potential result of climate change and interannual variability to help assess trends.

KEYWORDS

remote monitoring, endangered species, marine megafauna, conservation, Marine Protected Area (MPA), Western Indian Ocean (WIO), marine turtle, *Chelonia mydas*

INTRODUCTION

Population estimates are essential to make informed and effective management decisions (Nichols 2014), yet accurate estimates are difficult to obtain for many animal groups that are elusive or rare (Mcdonald 2004). Many studies rely on traditional capture-mark-recapture (Labonne and Gaudin 2005), ground (Udevitz et al. 2006), or aerial counts (McCarthy et al. 2022). These methods can be labour-intensive, expensive, or logistically challenging, particularly in remote locations. Additionally, capturing animals is invasive and can influence behaviour and biases results (Fieberg et al. 2015). Hence, non-invasive techniques that simultaneously reduce effort and cost are of interest (Pauli et al. 2010).

Marine megafauna populations are particularly difficult to assess given that most undertake vast migrations across oceans and spend the majority of their time offshore (Hays et al. 2016). Some animals provide an opportunity to be ‘captured’ when they come ashore to breed or rest (e.g., seals; Southwell et al. 2008, penguins; Southwell et al. 2013, and turtles; Lasala et al. 2023). Ideally sea turtle nesting beaches would be surveyed frequently and systematically to intercept all nesting females, but this is not possible at extensive sites with limited resources or at remote destinations and so in these cases, estimates are made from infrequent track and nest counts (Girondot 2017; Whiting et al. 2013).

Although originally for hunting, camera traps are now used to answer a wide range of ecological questions (Hamel et al. 2012). Cameras can remain in the field for months (dependent on settings), minimising resources and disturbance (McCallum 2012). They are non-invasive, reducing the risk of stress or harm to animals (Janečka et al. 2011) and operate day and night in harsh conditions for surveying of remote locations (Rowcliffe et al. 2014). While initially expensive, they are economical long-term as they can often be used for multiple seasons, studies, species, and interactions (Welbourne et al. 2020). Camera trap research focusses on elusive terrestrial mammals, using an automatic trigger function to capture animals passing by (Lyet et al. 2023) and some animals have unique markings enabling identification of individuals for density estimates, such as tigers identified by their unique stripes (Royle et al. 2009). However, there are approaches to obtain population estimates which do not require individual recognition (Rowcliffe et al. 2008; Palencia et al. 2021). Research has been undertaken to refine sampling methods and design to ensure the reliability of results which may change depending on camera model, settings, species, and habitat (Hamel et al. 2012; Palencia et al. 2021).

Specifically in sea turtle research, camera traps have been used to identify predators of nesting turtles, for example, Jaguar (*Panthera onca*) in Costa Rica (Fonseca et al. 2020), invasive rat (*Rattus rattus*) predation of turtle hatchlings in French Polynesia (Gronwald et al. 2019) and nest predation by yellow spotted goannas (*Varanus panoptes*) in Australia (Lei and Booth 2017b). They have also been used to assess predator behaviour patterns (Guilder et al. 2015), and strategies for nest protection (Lovemore et al. 2020). To our knowledge there are no published studies on the use of camera traps for assessments of nesting turtle populations.

Populations are often assessed using a single method, but the concept that a combination of techniques can complement and enhance data quality is increasingly acknowledged in conservation (Zwerts et al. 2021). Combining survey techniques allows us to fill knowledge gaps by creating a broader perspective, increase sample size, and increase data quality as the simultaneous use of two or more methods improve detection rates and spatial and temporal coverage (Rahman and Rahman 2021).

Given the increase in camera trap use and the need to assess sea turtle populations at remote locations with increased temporal coverage, in this study we investigate how camera traps can be used to estimate nesting turtle populations at a key green turtle (*Chelonia mydas*) nesting site within a Marine Protected Area (MPA) in the Western Indian Ocean (WIO). We demonstrate how camera traps can be used for population estimates validating our results from foot patrol surveys. Additionally, we show how simulated data was used to determine suitable camera trap coverage on nesting beaches to record a representative track count to apply this method to nesting sites around the world with different beach length and density of tracks. Further we show how camera traps can be used to estimate track longevity, tidal influence on track counts, and interannual variations including changes in nesting season as a potential result of climate change.

MATERIALS AND METHODS

Study area

Diego Garcia (7.42°S, 72.45°E) is the largest and only inhabited island in the Chagos Archipelago and has 72.1 km of coastline of which 40.5 km (56 %) is deemed suitable nesting habitat (Mortimer et al. 2020). Our study was undertaken on the south-eastern arm of Diego Garcia, along a 2.8 km stretch of the beach deemed the index beach, which has been identified as one of the highest nesting density areas on the island (Fig. 6.1a; Mortimer et al. 2020). Green turtles nest here year-round but mostly between June and October with a peak in August, whilst hawksbill turtles nest between October and February (Mortimer et al. 2020).

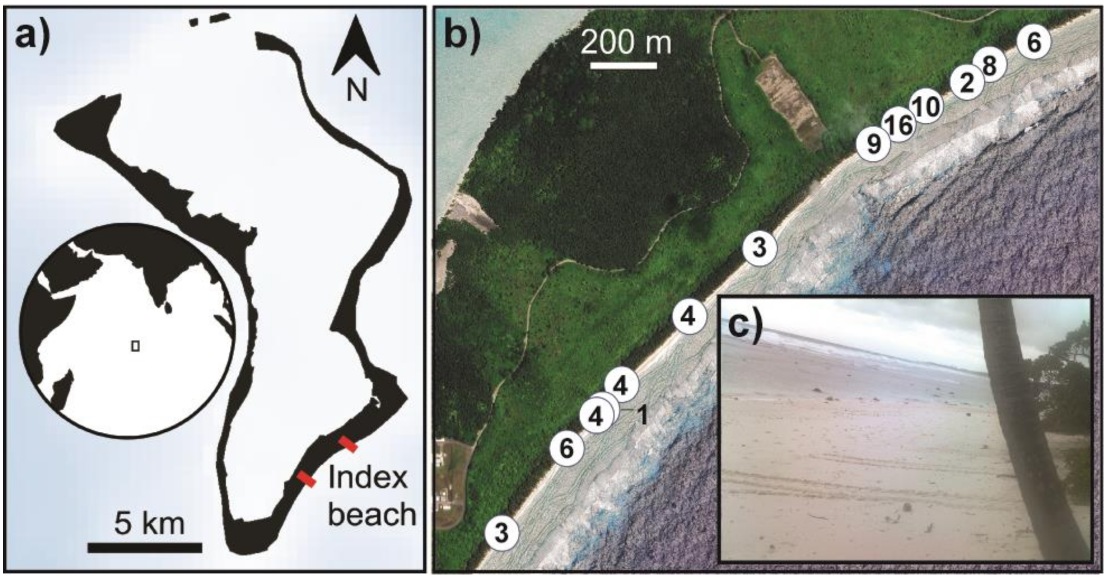

Figure 6.1. a) Diego Garcia (source: GEBCO, 2021) and inset map showing the location of the Chagos Archipelago (black rectangle) in relation to the wider Indian Ocean. **b)** The location of camera traps along the index beach (between red lines) located on the southeast coast of Diego Garcia. Numbers represent the number of tracks recorded by each camera trap across April to September 2021 and July and August 2022 to understand the distribution of tracks across the nesting beach. Basemap from Google satellite imagery sourced through QGIS3. **c)** An example of a camera trap image with sea turtle tracks.

Foot patrol surveys

We collected data from foot patrol surveys by walking the index beach on Diego Garcia to record turtle tracks. Tracks are defined as the imprint a turtle leaves behind after crawling on the sand (Fig 6.1c). The surveys were conducted during the months of April and May 2021 and August 2022 (14, 13, and 21 days of surveys within the month, respectively). For every survey, all tracks were counted, and a line drawn through the track to avoid double counting. Mean track width was recorded from three measurements using a flexible tape measure and, along with characteristics of the track, used to identify turtle species.

Tidal influence

To understand the influence of tides on track counts, we assessed the number of track counts from foot patrol surveys along the tidal cycle as the number of days after spring tide. Spring tide being the highest tide with the greatest tidal range on or after the most recent full or new moon. We split days after spring tides into days around neap tide (days 4-11) and days around spring tide (days 0-3; 12-14) to make a comparison between the number of tracks counted during neap tides and spring tides. We used one full tidal cycle in the middle of each month and filled in gaps for the foot patrol surveys to assign track counts to specific days. On the days where there was no survey the day before a survey day any tracks > 24 hr were recorded on the 'no survey day' and any tracks < 24hr were recorded on the survey day. If there were two days between surveys, then tracks > 24 hr were split evenly across the two days or if there was an odd number then more tracks were added to the day before the survey (e.g., if there were three old tracks then two were assigned to one day before the survey and one track to two days before the survey day). In the instance of three days between survey days over neaps, the same principle was used, for example, if there were four tracks to cover three days of no surveys then two tracks were assigned to the day before the survey and one track to two days before the survey and one track to three days before the survey.

Camera trap survey design and settings

Camera traps (model Apeman H70; n = 13; with 32GB SD cards and lithium-ion batteries) were set up along the 2.8 km Index beach in Diego Garcia (Fig. 6.1b). A pilot study was conducted between 2018-2019 using various camera trap models (e.g., Ereagle Wildlife Trail Camera 12MP 1080P, Campark Trail Game Camera 12MP 1080P) to test image quality and robustness. Camera traps were set up on vegetation (e.g., *Cocos nucifera; Tournefortia;* Fig. S6.1a) pointing down the length of beach where possible or slightly towards the sea depending on vegetation obstruction (Fig. S6.1b). Trigger settings were disabled to prolong battery life and camera traps were set to take photographs every 30 min daily between 0700 and 0830 hr to increase the chances of capturing a clear image. The distance observed from each camera trap was measured by creating 'turtle tracks' in the sand every 5m until the tracks were no longer visible in the images (range from a single camera trap = 5-30 m; Fig. S6.1b).

Camera trap image processing and track count

Images were processed using a 4k monitor and data recorded from each image included camera trap ID, date, track count, track longevity, day after spring tide, distance observed from camera trap. A turtle emergence was classified if there was a single track or a track up and down the beach visible from the camera trap. Tracks were identified as up and down from the direction of the flipper 'scuff' marks in the sand. We assume all tracks to be green turtle tracks as the tracks observed during foot patrol surveys were all green turtle tracks and surveys occurred outside of the hawksbill turtle nesting season.

For each day where foot patrol and camera traps were running parallel (n = 91), raw camera trap track counts were extrapolated to the whole index beach using the following formula:

Index beach distance / distance covered by camera traps * raw camera trap track counts.

To calculate track longevity (the number of days a turtle tracks persists on the beach), we used camera trap images from April to September 2021 and July and August 2022 around the peak green turtle nesting season. Track longevity was recorded for each track unless the track was already present on the first day images started recording or if the camera stopped working when a track was still present. Mean track longevity was calculated across both spring and neap tides together and just over days around neap tides (4-11 days after spring tide) and just over days around spring tides (0-3; 12-14 days after spring tide).

The clarity of some images was affected by fog, glare, and darkness and we simply categorised these into good visibility and poor visibility (unable to see the sand clearly and count tracks from images). During image processing, it was evident that the distance from some camera traps had changed over time due to weather conditions and obstructions that altered the view. We therefore reanalysed and estimated new distances from each camera trap image.

Simulation to assess optimal beach coverage by camera traps

We assessed how the extent of beach coverage with camera traps might be expected to effect the confidence in the estimate of the mean number of tracks per day. To do this we ran a simulation parameterised by the length and typical number of tracks on our study beach. We assumed a beach length of 2.8 km long. We assumed that the mean number of tracks per day was 6. Then for each 1 m section of beach for each day, we randomly picked if that 1 m would include a track from a binomial distribution with the probabilities of no track (p) and a track (q), being p = 0.9978572 and q = 0.0021428. Then we randomly selected a percentage of the beach that would be covered by camera traps and assessed how many of the tracks would be captured by the cameras each day. We ran the model for 90-d and worked out the mean number of tracks counted by the cameras for those 90-d and then extrapolated up to the mean number of tracks for the whole beach. For each value of beach coverage by the cameras, we ran 100 simulations (each simulation was 90-d) and then from those 100 simulations worked out the SD of the estimated track count for the entire beach. We varied the percentage of the beach covered by the cameras (n = 13) from 2 % to 40 %.

Data analyses

An exponential decay formula using log-standard deviation was fitted to the standard deviation by camera trap coverage data. A t-test was used to test if there was significance in the model simulated mean track counts and the assumed mean number of 6 tracks per day. All plots were created, and statistical analyses conducted in R (R Core Team; version 4.2.2).

RESULTS

Tidal influence on nesting emergences

From foot patrol track surveys, we observed a bimodal distribution of tracks with peaks either side of neap tide across some tidal cycles (April 2021 and August 2022). We observed an increase in tracks during neap tides between 4-11 days after spring tide (mean = 6.4; SD = 4.5; n = 165 tracks) and a decrease in tracks during spring tides between 0-3 and 12-14 days after spring tide (mean = 3.5; SD = 3.3; n = 74 tracks; Fig. 6.2).

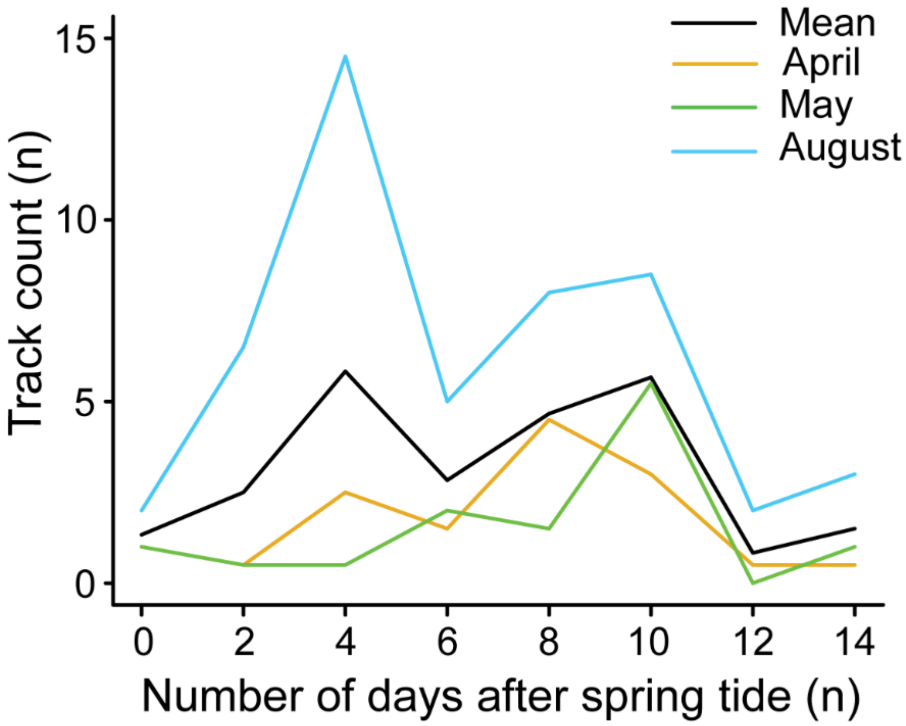

Figure 6.2. Track counts from foot patrols were higher during days around neap tide compared to days around spring tide. Track count from foot patrol surveys across the days after the spring tide in April and May 2021, and August 2022, and the mean across all months. Spring tide (0) being the highest tide with the greatest tidal range on or after the most recent full or new moon. We split days after spring tide into days around neap tide (days 4-11) and days around spring tide (days 0-3; 12-14). Across some tidal cycles track counts show a bimodal distribution with a peak in counts either side of the neap tide.

Tidal influence on track longevity

From camera trap images, we calculated track longevity across days of neap and spring tides (mean = 3.8 days; SD = 2.2; range = 1-10 days; n = 74 tracks) and by neap and string tides separately. Track longevity was higher during neap tides (mean = 4.1; SD = 2.2; range = 1-10 days; n = 41 tracks) compared to spring tides (mean = 3.1; SD = 2.2; range = 1-9 days; n = 33 tracks).

Foot patrol and camera trap track count comparison

Due to the likelihood of tracks being washed away during spring tides and potentially missed by the camera traps, we compared track counts from foot patrols and camera traps during neap tides as well as from the full tidal cycle. Across the 91 days where foot patrol surveys and camera traps were running parallel, from foot patrol surveys alone (47 total days on the beach) we recorded 239 tracks of which 43 were recorded in April 2021, 52 in May 2021 and 144 in August 2022. The mean number of daily tracks recorded across the 91 days (full tidal cycle) was 5.1 (SD = 4.2; range = 0-19; n = 239 tracks), whereas during neap tides only the mean number of tracks per day was 6.35 (SD = 4.5; range = 1-19; n = 165 tracks). All tracks encountered were from nesting green turtles.

From camera traps alone, 21 tracks were observed between April and May 2021 and August 2022. For each day across the full tidal cycle (n = 91), raw camera trap track counts were extrapolated to the whole index beach and the mean track count was 3.7 (SD = 8.5; range = 0-43.1; 339.3 tracks). When solely looking at track counts during neap tides (4-11 days after spring tide; n = 43 days) the mean track count was 5.3 (SD = 9; range = 0-38.6; n = 264.2 tracks).

Camera settings

As the trigger function was disabled on our camera traps, and they were set to capture daily images (n = 4) on the beach every morning, we prolonged the battery life and extended the length of time the cameras could remain working in the field for up to six months with no servicing. Capturing multiple images meant we increased the chances of obtaining a clear image each day for track analysis. From images available for functioning cameras across the 91 days in April and May 2021 and August 2022, 94 % (968 out of 1025) of the images had good visibility.

Simulation to assess optimal beach coverage by camera traps

Covering an adequate amount of the nesting beach is a key factor in the success of using camera traps on nesting beaches. We explored the effect of increasing the number of camera traps and found that as the extent of the beach covered by cameras increased, sampling variation decreased for the estimated mean number of tracks per day over a 90-d simulation (standard deviation = 1.4032*exp(0.0347*coverage; R^2 = 0.82; n = 6; $F_{1,4}$ = 23.82; $p < 0.01$; Fig. 6.3a). For example, when the camera traps covered 10% of the beach, while the mean number of tracks for the 90-d simulations (6.08) was not significantly different from 6 (t_{99} = 0.95; p = 0.34), the SD was 0.8618, i.e. 95 % of the estimated mean daily number of tracks were between 4.393 and 7.771 tracks per day (Fig. 6.3b).

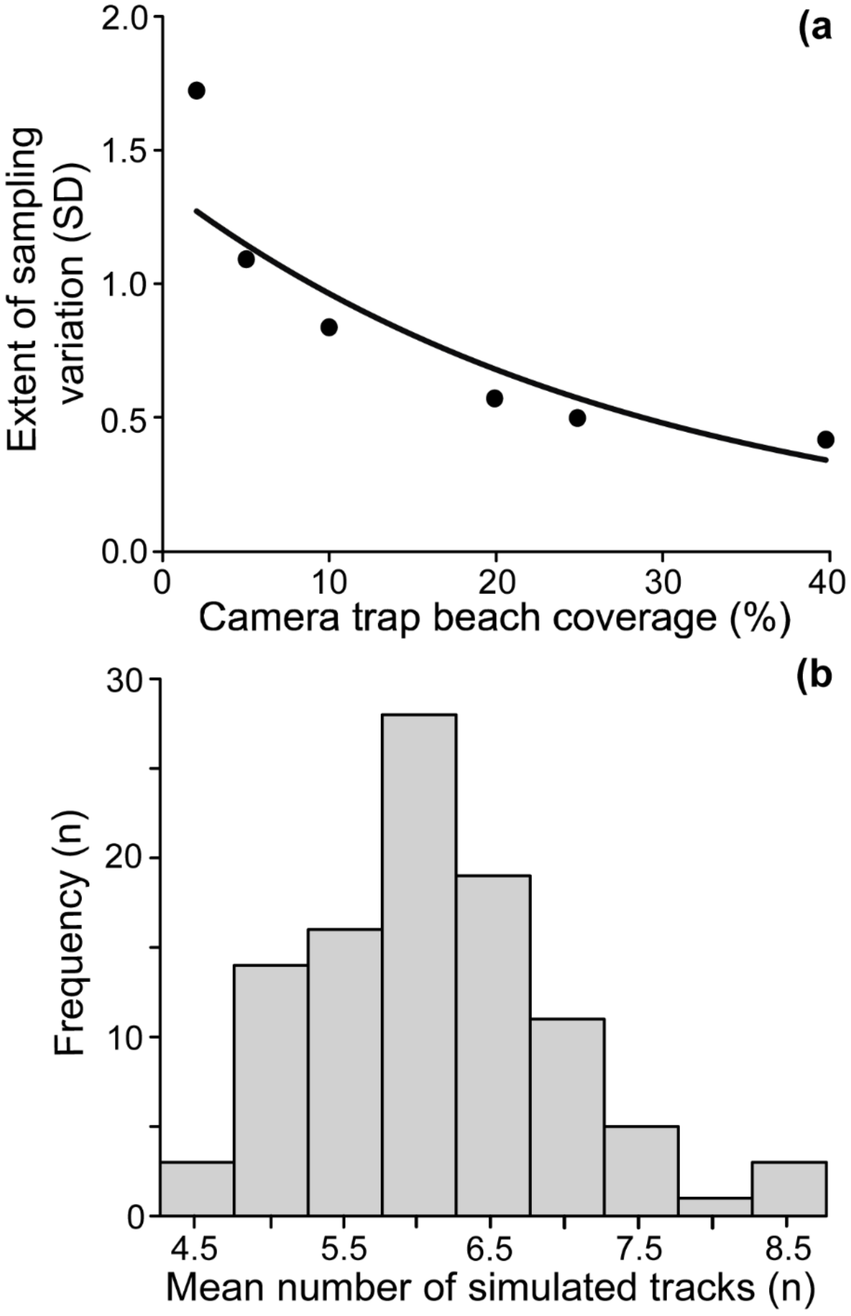

Figure 6.3. Camera trap beach coverage influences the reliability of track counts **a)** The standard deviation for the estimated mean number of tracks per day over a 90-d simulation when there were different extents of beach coverage by cameras. As the extent of beach coverage increased, the SD of the estimated mean number of tracks per day decreased (standard deviation = 1.4032*exp (0.0347*coverage; $R^2 = 0.82$; $n = 6$; $F_{1,4} = 23.82$; $p < 0.01$). **b)** An example of range of values for the mean number of tracks per 90-d simulation, repeated 100 times. In this case 10% of the beach was covered by cameras and the SD for the mean number of tracks was 0.86.

DISCUSSION

By applying the novel approach of camera traps combined with foot patrol surveys on sea turtle nesting beaches, we demonstrate how camera traps can be validated and used for population estimates and to improve understanding of emergence patterns of nesting turtles at an important rookery in the Western Indian Ocean. This finding is noteworthy given that many sea turtle nesting datasets are temporally fragmented (Omeyer et al. 2022) due to varying efforts from foot patrol surveys within and across years and locations, particularly at remote, or extensive sites (Bell et al. 2007; Shimada et al. 2021), and how camera traps can fill this gap having the ability to remain in field long-term. Moreover, as nesting numbers (Broderick et al. 2001; Mazaris et al. 2017; Hays et al. 2024) and nesting beach length varies (Kikukawa et al. 2001), we show how camera traps can be applied to other nesting sites around the world.

We report that track counts from foot patrol surveys and camera trap surveys were comparable. Although camera traps did not provide the exact counts foot patrol surveys did, they are within the same order of magnitude and so track counts from camera traps can be used as a proxy to assess an increase or decrease in population over time. In a similar manner, several well-designed studies have assessed trends in sea turtle populations from foot patrol time series data (Mazaris et al. 2017; Hays et al. 2024). As nesting females generally do not breed every year (Broderick et al. 2003) there is often substantial interannual variability in sea turtle nesting numbers, that could be as much as 60-fold between successive years (Hays et al. 2022b) that influences trend assessments and so given that there is already interannual variability in nesting numbers the difference between camera trap and foot patrol track counts is negligible. For populations where interannual variability greatly influences the ability to detect trends, data across two or three consecutive years can be averaged (Mazaris et al. 2017) and so the same could be applied for data obtained from camera traps.

As the use of camera traps for wildlife ecology has increased, three questions have been highlighted as key considerations for optimal experimental design: firstly, the number of camera traps sufficient for a study site; secondly, when should camera traps be set up and, thirdly, the length of time camera traps should be set up for (Kays et al. 2020).

For the first key consideration, to assess the number of camera traps required for optimal beach coverage, we investigated the variation in track counts in relation to varying sampling effort using simulated data and found that increasing the number of camera traps along the nesting beach (i.e., increased coverage) led to a decrease in sampling variation. Luo et al. 2020 developed a model taking into account space use and found that increasing the number of camera traps and duration of monitoring can increase the precision of estimates. The sampling effort required for such studies can be influenced by the size of species and their habitat use. For example, to detect terrestrial animals in an enclosed park, the effort (i.e., number of camera traps) needed to obtain a sufficient sample size varied by density and species range (Rowcliffe et al. 2008). In the case of our study on sea turtle nesting beaches, the length of the beach and track density influenced the required sampling effort. In Diego Garcia, with relatively low track density, around 10% coverage was sufficient, but our model can be extended to ensure coverage is optimal at other sites with longer or shorter beaches, or beaches with higher or lower track densities.

To address the second and third key considerations and for decision-making about camera set up and duration of study in the context of nesting sea turtle emergences and population estimates, it is important to consider nesting seasonality and the duration of the nesting season which can vary year to year (Mrosovsky et al. 1984), by species (Mortimer et al. 2020) and location (Dewald and Pike 2013). To estimate annual nest abundance for track count foot patrol data, Whiting et al. (2013) created simulation models that showed a five-to-seven-fold greater monitoring effort was needed for longer nesting seasons. With that in mind, although spatial coverage is reduced, camera traps can ideally be used to increase the monitoring effort temporally for longer nesting seasons, which could range from four months for hawksbills to year-round for green turtles at our study site in Diego Garcia (Mortimer et al. 2020).

The third consideration of the length of time camera traps should be set up for can also largely depend on the remoteness of the location and frequency of camera servicing in relation to settings and camera trap battery life. Elements influencing the operating duration of cameras include camera settings, battery life, storage card capacity, and weather conditions (e.g., rain affecting the clarity of images or causing accumulation of dirt on the lens). Camera trap studies focussing on terrestrial animals opt for trigger function settings to capture animals passing by (Lyet et al. 2023). For example, to count, identify and evaluate relative abundance indices of terrestrial herbivores in the Serengeti National Park (Palmer et al. 2018). However, as sea turtles crawl on the beach, they leave an identifiable track in the sand as an indication of their presence, and so we did not think a similar approach would be necessary and instead chose to photograph the beach to capture tracks after sunrise every morning rather than photograph individuals. In doing so, we extended the battery life and consequently the length of time camera traps could remain in field without servicing.

With the settings to capture four images per day, we increased the chances of a clear image for observing tracks. As we disable the trigger function which prolongs the battery life, we recommend servicing camera traps (change batteries and SD cards) and assessing any damage (replace cameras or attachments if necessary) at least every six months. For any remote image monitoring technique, steps can be taken to capture images with little interference, for example, setting cameras to face north and south to avoid glare from sunrise and sunset, yet this is not possible in all situations and the clarity of images can be influenced by glare, fog, and precipitation (Madsen et al. 2020).

There is a lack of temporal coverage at remote nesting beaches with either opportunistic foot patrol surveys (e.g., Cocos Keeling; Whiting et al. 2014) or aerial surveys conducted by plane or Uncrewed Aerial Vehicles (UAVs; Marsh and Saalfeld 1989; Dunstan et al. 2020). Although snapshot foot patrols provide more detailed nesting information and aerial surveys increase spatial coverage, there is minimal temporal coverage to detect changes within the nesting season, for example, potential shifts in nesting due to climate change (Hawkes et al. 2007) or between seasons to explore interannual variability (Omeyer et al. 2022). Our camera trap findings address the issue of minimal temporal coverage at these remote locations to detect patterns and changes throughout the nesting season. When only part of the nesting beach or area is surveyed from foot patrols, counts are extrapolated to the whole suitable nesting area (Mortimer et al. 2020). In the same way, using our findings from camera traps, complete temporal coverage is possible, even if with limited spatial coverage, as counts can be extrapolated from areas covered by the camera traps to the whole nesting beach. Additionally, a combination of snapshot foot patrol surveys, aerial surveys (UAVs, planes, or satellite imagery; Casale and Ceriani 2019) and camera traps could be used to acquire detailed nesting information and increased spatial and temporal coverage to understand nesting patterns and distributions at remote locations.

Turtle emergences and nesting sites are often not uniform along the nesting beach and reef and beach geomorphology can influence where a turtle emerges from the sea onto the beach and where a turtle decides to attempt or successfully nest (Cuevas et al. 2021). For example, at Ascension Island it has been suggested that green turtle emergence locations are influenced by the offshore topography (Mortimer 1982). Similarly, in Texas, Kemp's Ridley (*Lepidochelys kempii*) nesting hotspots were found along the central section of Padre Island likely influenced by elevation and distance from the shoreline (Culver et al. 2020). For sites where track distribution is known, the pattern of emergences and hotspots should be highlighted and incorporated into the design of camera trap studies for abundance estimates to avoid over estimations when cameras are set up solely in hotspots and vice versa. For example, inappropriate camera placement at Whipsnade Wild Animal Park led to an underestimate of mara (*Dolichotis patagonum;* Rowcliffe et al. 2008). For sites where track distribution is unknown, likely at remote locations, camera traps can be setup on beaches specifically to understand the distribution of emergences. From our camera trap images we found that track counts were variable along the beach, however the data could be explored further to understand variability of track distribution along the beach across months and between seasons. Additionally, cameras can be used to monitor changes in hotspots as changes in reef and beach geomorphology over time could influence track and nest distribution.

The influence of tidal phase on emergence and nesting effort has been reported from some regions and for several species, for example leatherback turtles (*Dermochelys coriacea*) tended to avoid high and low tides across the tidal cycle on the Caribbean coast of Costa Rica (Palomino-González et al. 2020). We report a different tidal pattern where green turtle emergences increase during neap tides and decrease during spring tides. Likewise, Witt et al. (2009) used aerial surveys in Gabon to show an increase in nesting effort by leatherbacks during days around neap tides. Similarly, studies of olive ridley (*Lepidochelys olivacea*) solitary and arribada nesting events in Costa Rica reported more females emerge during the weaker neap tide phase of third-quarter moon than any other moon phase (Dornfield et al. 2014; Bézy et al. 2020). On the other hand, leatherback peak nesting occurs around spring tides in French Guiana (Girondot and Fretey 1996). Regional differences may be attributed to site characteristics (e.g., topography of the beach or tidal patterns such as diurnal or semidiurnal tides). We highlight the importance of understanding patterns of emergence and or nesting effort at specific sites around the world to effectively apply correction factors when designing a camera trap study to calculate population estimates from limited track counts.

An understanding of track longevity is important for accurate population size estimation. Track longevity varies considerably across beaches due to substrate and climate, and between species, for example ranging from 10 days from June to October and 14 days across other months for green turtle tracks on Aldabra, Seychelles (Gibson 1979). Weather (rain and wind) and tides can all influence the longevity of turtle tracks on the beach. For example, in Cyprus the hot settled weather and lack of rain results in good track preservation and visibility between surveys (Omeyer et al. 2021). Tracks are known to persist around neap tides and wash away quickly around high spring tides (Shoop et al. 1985). From camera trap images, we were able to calculate track longevity and as expected found that tracks persisted for longer during neap tides (mean of 4.1 days) compared with spring tides (mean of 3.1 days). When combining tracks over both neap and spring tides, track duration was 3.8 days, which reflected estimates of mean track longevity of 3.9 days from foot patrols during another season at our site (Mortimer et al. 2020). The positive comparison of our camera trap findings to foot patrol longevity estimates validates the use of camera traps to estimate track longevity effectively. Although, foot patrol and camera trap track longevity estimates were similar, camera traps can assess track longevity across the whole nesting season, covering multiple tidal cycles, and weather conditions when foot patrols are not available.

For nesting beaches with one sea turtle species, there is no concern around the track identification in camera trap photographs. However, on beaches with multiple species nesting, track identification adds an element of complexity, and so it is important to consider the difficulty of differentiating tracks from different species from remote camera images (e.g., remote sensing imagery, camera trap images, UAV images, Potter et al. 2018; Wang et al. 2019). Although hawksbill and green turtles nest on Diego Garcia, our study took place outside of hawksbill nesting season (Mortimer et al. 2020) so that we were very confident (supported by foot patrol survey observations) that all tracks recorded by camera traps were from green turtles. Active deep learning systems have been incorporated into camera trap image analysis for many terrestrial animal studies decreasing the time for observers to manually identify animals and annotate images (Norouzzadeh et al. 2020). However, these systems differentiate between animals that are quite distinct from one another rather than similar size and shape species. For our study, we are specifically observing tracks over individuals. Nonetheless, *in situ*ations where camera traps may be used at times or locations where multiple species nesting overlap, species ratios from ground surveys may be applied. Green and hawksbill tracks are distinct from one another, but we observe these differences through close inspection of the tracks during foot patrol surveys, where track characteristics can be identified to distinguish between species. We can also collect track widths and distinguish between species as green turtle tracks are wider (> 100 cm wide) than hawksbill turtles (Mortimer et al. 2011). Given the horizontal angle of camera traps, it would be difficult to obtain positive identification from all tracks and so species ratios from ground truthing via foot patrols could be applied. For example, Stokes et al. (2023) compared species ratios from physical turtle captures and UAV surveys (using length to width ratios to identify species) and the results were similar across the two methods. A similar approach could be applied to camera traps using the ratio of species from foot patrols to allocate tracks on images where species cannot be determined.

In summary, our study validated the use of camera traps for sea turtle population estimates and emergence activity as a feasible and affordable method in remote locations. We highlight that foot patrol surveys are necessary for detailed nesting data (e.g., to count successful nests, clutch counts and excavations for hatching success), environmental data and providing ground truthing and validation of remote surveys (e.g., aerial, satellite, and camera trapping). However, camera trapping can be used as a new tool in remote or frequently inaccessible areas for population estimates, emergence patterns, shifts in nesting seasons and interannual variability for trend assessment where little to no assessments would otherwise be possible. The extended application of our method depends on study site characteristics, including length of the nesting beach, nesting density, and multiple species nesting. Yet, simulations can be run to design the optimal coverage of camera traps for a specific site. The advantage of camera traps is the increased temporal coverage at remote locations to assess changes within and between the nesting season, including early shifts in nesting which could occur from climate change. We encourage the use of camera traps on nesting beaches around the world to further test this approach at sites with varying conditions.

Acknowledgements

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CHAPTER SEVEN: Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species

This chapter was amended from published work:

Stokes HJ, Mortimer JA, Laloë J-O, Hays GC, Esteban N (2023) Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. Ecosph 14:e4444. https://doi.org/10.1002/ecs2.4444

Disclaimer: NE and GCH conceived the study. NE, HJS, JAM and J-OL completed the fieldwork. HJS led the data analysis. HJS, GCH and NE led the writing with contributions from all authors.

ABSTRACT

Estimating population abundance is central to many ecological studies and important in conservation planning. Yet the elusive nature of many species makes estimating their abundance challenging. Abundance estimates of sea turtles, marine birds and seals are usually made when breeding adults are ashore, while life-stages spent at sea, including as juveniles, are often poorly sampled. We used a combination of high-resolution satellite tracking (Fastloc-GPS), Uncrewed Aerial Vehicle (UAV) surveys and capture-mark-recapture approaches to assess the abundance of immature hawksbills (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) in a tidal lagoon of the Chagos Archipelago (Indian Ocean). We captured, marked, and released 50 turtles (48 hawksbill and 2 green turtles) prior to UAV surveys and used satellite tracking data from 27 immature turtles (25 hawksbill and 2 green turtles) to refine the estimated numbers of marked turtles available for resighting and those likely to have emigrated from the study area. We estimated a total of 339 turtles in the lagoon with a density variation at different tidal heights between 265 turtles per km^{-2} at high water and 499 turtles km^{-2} at low water. Of these 91% were hawksbills and 9% were green turtles. These hawksbill densities are the highest reported amongst 17 foraging sites recorded around the World, and likely reflect successful long-term protection of turtles in the Chagos Archipelago.

KEYWORDS

Endangered species; UAV; marine megafauna; shifting baseline; density; mark-resight; satellite tracking; conservation; Marine Protected Area (MPA)

INTRODUCTION

Population estimates are integral to conservation planning, for example to allow high-use areas to be defined and populations trends to be assessed (Lotze et al. 2011; Santini et al. 2018) and various census techniques have been widely used. Capture-Mark-Recapture (CMR) or Captue-Mark-Resight are classic approaches, in terrestrial (Lindberg 2012), freshwater (Carey et al. 2019) and marine (Bradshaw et al. 2007) systems. Sometimes census data involve direct counts of animals visible onshore, such as nesting seabirds or seals with pups (Clarke et al. 2011; Russell et al. 2019). In other cases, a population is sampled and numbers or biomass per unit effort are recorded, as in plankton, benthos, and fisheries surveys (Keller et al. 2010; Dutta et al. 2016). Yet despite the broad success of these approaches, in some cases census data remain difficult to obtain, such as for elusive, rare, or widely distributed species or life-history stages (e.g. beaked whales; Hildebrand et al. 2015). Obtaining census data in such cases is increasingly facilitated by modern technology and the development of new approaches. For example, camera traps are now widely used for elusive species such as cheetahs (*Acinonyx jubatus*; Brassine and Parker 2015) and otters (e.g. Eurasian otter, *Lutra lutra*; Gil-Sánchez and Antorán-Pilar 2020), and thermography for elusive species (e.g. brown hare leverets, *Lepus europaeus;* Karp 2020). Uncrewed Aerial Vehicle (UAV) surveys allow for ease of sampling expansive areas (Koh and Wich 2012).

Here we develop an approach that combines UAV surveys, CMR estimates, and high-resolution satellite tracking data to produce abundance estimates for a little-known life-stage of a critically endangered species. We also highlight the value of this synergistic use of these three methods for population estimation surveys across varied taxa. Sea turtles are a group for which information on the abundance of certain life-stages remains scant. While the abundance of adult females is routinely measured using counts of nests or tracks on nesting beaches (Mazaris et al. 2017), the abundance of male turtles and the juvenile life stages are poorly known and filling this knowledge gap is a key issue for sea turtle ecology and conservation (Rees et al. 2016; Wildermann et al. 2018). While nesting numbers of some species and populations of sea turtles have shown encouraging upward trends (Mazaris et al. 2017), the hawksbill turtle (*Eretmochelys imbricata*) is listed globally as critically endangered (Mortimer and Donnelly 2008). Therefore, understanding the population status of intractable life history stages of this species is fundamental for identifying priority conservation regions and habitats, as well as for measuring population status at protected sites. Here we examine the abundance and density of immature hawksbill turtles at a site that has been well protected and free of negative anthropogenic impacts for many decades.

METHODS

Study site

Diego Garcia is the largest and only inhabited island in the Chagos Archipelago in the Indian Ocean. Research was undertaken at Turtle Cove (7.4309 °S, 72.4349 °N) situated in the south of Diego Garcia lagoon, which is a Ramsar site. Maximum depth at the cove entrance is 3.22 m (measured using a G5 logger, CTS, UK, from 5 February to 10 August 2021). Turtle Cove provides foraging habitat for immature hawksbill and green turtles (*Chelonia mydas*) and both species have been protected by conservation legislation since 1968 and 1970, respectively (Mortimer et al. 2020; Fig. 7.1).

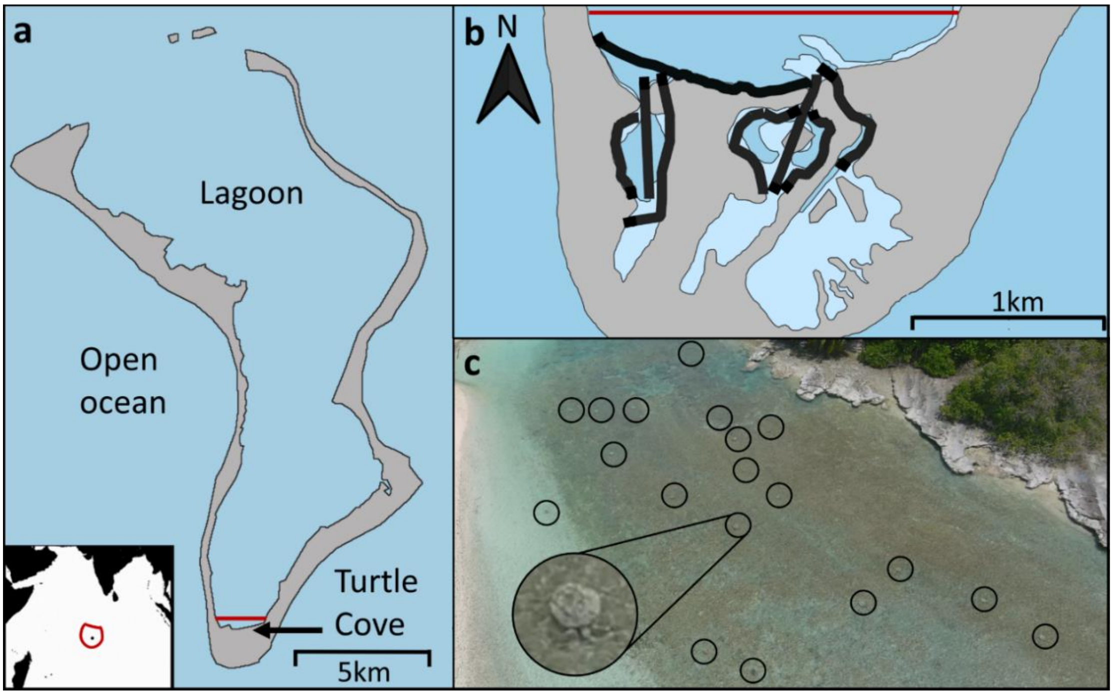

Figure 7.1. a) Diego Garcia with an inset map of the Chagos Archipelago in relation to the wider Indian Ocean including the British Indian Ocean Territory (BIOT) Marine Protected Area and Exclusive Economic Zone boundary (red line); **b)** Uncrewed Aerial Vehicle (UAV) Flight paths (black) over Turtle Cove showing areas exposed at low water (light blue) and the boundary of Turtle Cove (red line). **c)** Image of turtles (black circles) from the UAV at 30 m altitude.

Physical captures and marking turtles

In February 2021, turtles were captured by hand, following methods detailed in Hays et al. (2021b). Straight carapace length notch-tip (SCLn-t), straight carapace width (SCW), curved carapace length notch-tip (CCLn-t) and curved carapace width (CCW) (Bolten 1999) were measured for all captured turtles. These measurements add to our morphometric dataset (compiled since 1996) along with CCL from nesting hawksbill (n = 23) and green turtle (n = 49) females since 2012. Captured turtles were marked with a broad line or cross of white paint on the carapace, following procedures outlined in Dunstan et al. (2020) and released back into Turtle Cove within 2 hr of capture. Field observations showed the paint was clearly visible on the carapace for up to two weeks.

Satellite tagging

UAV surveys were conducted within five days of marking turtles and counts of marked versus unmarked turtles were made. In theory, turtles might leave Turtle Cove within five days of release and so would not be available for resighting within the UAV surveys. To estimate what proportion of turtles would leave Turtle Cove within 5 days of release, we used high-resolution tracking data from 27 immature turtles (25 hawksbills; 2 greens) equipped with Fastloc-GPS Argos tags (SPLASH10-BF-297B-01, Wildlife Computers, Seattle, Washington, USA) at the same site between 2018 and 2021 (see Hays et al. 2021a for satellite tag attachment details). Fastloc-GPS locations were filtered, by excluding residual values > 30 and locations with < 5 satellites, to improve accuracy. During days 1-5 after release, we calculated the percentage of time satellite-tracked turtles spent inside and outside of Turtle Cove.

UAV surveys

A quadcopter UAV (Autel Robotics EVO II, United States) recording 4K UHD videos at 30 frames per second (fps) was flown by NE, a licenced UAV operator. As per safety guidelines, an observer was present for each flight to assist the pilot. Flights were manually flown at 5 $m.s^{-2}$, although flight speed fluctuated due to factors including wind and obstructions. Transect lengths varied to accommodate for the shape and conditions of each cove. A pilot study was conducted in 2018 to establish the best conditions to undertake surveys at Turtle Cove and initial analysis of data informed our 2021 survey design. Flight altitude of 30 m was chosen to not disturb turtles (Bevan et al. 2016; Schofield et al. 2017a), while maintaining video resolution to identify turtles. Eight transects were flown repeatedly over three days in the late morning (on day 3 the survey was also repeated in the afternoon). The order of transects was altered during each survey period to cover each area during different tidal states. For each flight, metadata including dates, start and end time, and start and end coordinates were recorded. An anemometer was used on the ground to measure wind speed ($m\ s^{-2}$) before each survey. Tide state and times were obtained for Diego Garcia (National Tidal and Sea Level Facility, 2021). In some cases, the UAV was flown in both directions along a transect to determine which footage had the least sun glare. Where these repeat surveys were undertaken, the transect with the best conditions (e.g., low glare) was chosen to count turtles.

Video processing

Image analysis was conducted by one observer (HJS). Data recorded included turtle counts and absence/presence of markings (white paint and/or satellite tags; Fig. 7.2). For optimal analysis, UAV footage was processed on a 69 cm 4K ultra-HD monitor and a high-performance desktop with a high-quality graphics card. Adobe Premier Pro (Adobe, 2021) was used to aid in processing UAV videos and extracting high quality images. Videos were moved frame by frame when a turtle was detected to capture the clearest image. Turtles were assigned a category of confidence in detection (Certain, Probable or Possible; Fig. 7.2). Only turtles of the category "Certain" were included in our abundance and density estimations. UAV flight data were extracted using Airdata (Airdata UAV, 2021), an application for UAV flight logs and management. The area of each transect was measured by multiplying the length of the transect by the width of the frame (30 m), following the standard approach of strip transect analysis (Marsh and Sinclair 1989). Unavailable area in the footage was identified (e.g., over land, shadow), measured and calculated using the ImageJ polygon tool (Schneider et al. 2012) and subtracted from the total area when estimating turtle densities.

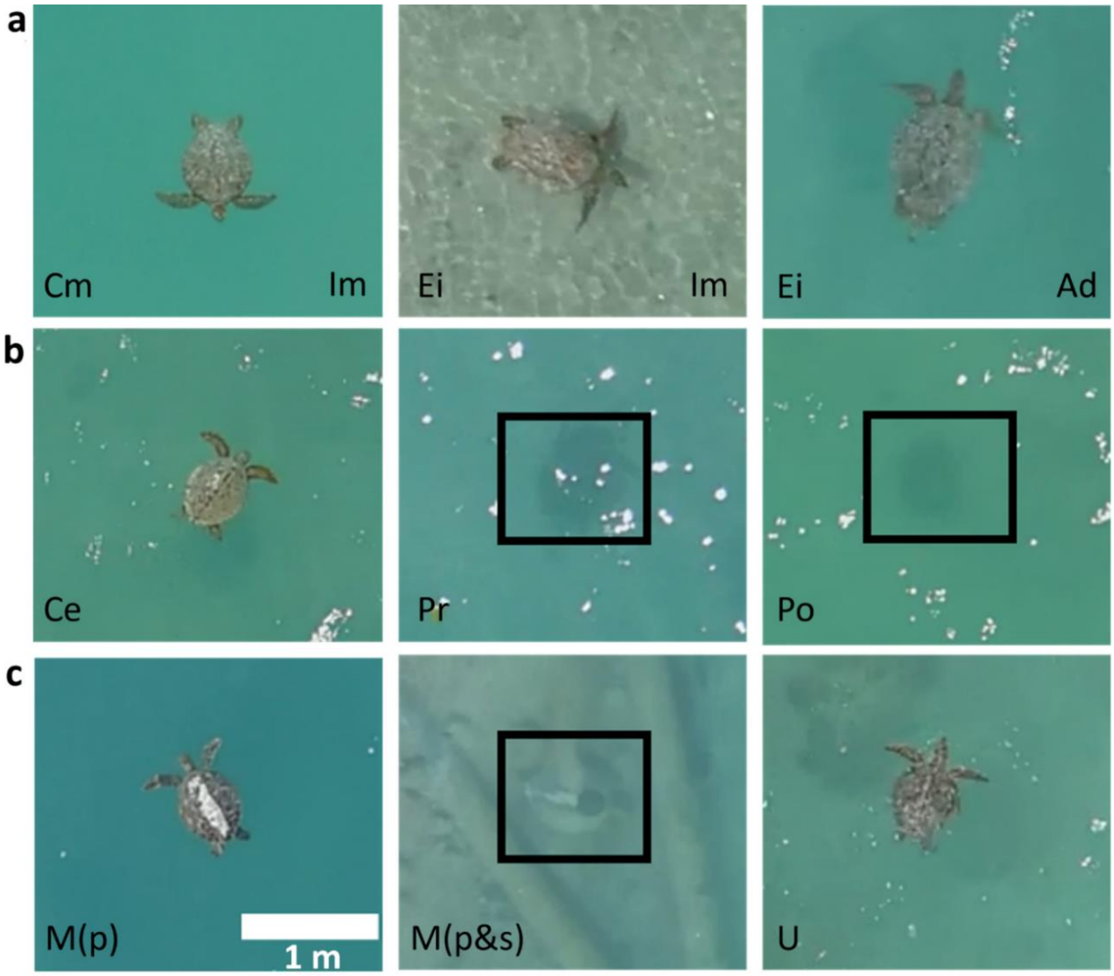

Figure 7.2. Examples of images from Uncrewed Aerial Vehicle (UAV) video surveys showing (**a**) an immature green turtle (Cm; Im), immature hawksbill turtle (Ei; Im) and an adult male hawksbill (Ei; Ad) turtle (**b**) Certain (Ce), Probable (Pr) and Possible (Po) turtles and (**c**) marked turtles with white non-toxic paint (M; p), paint and satellite tag (M; p&s) and an unmarked turtle. Images have been cropped. Scalebar applicable to all images.

Species identification

The length-to-width ratios (L/W) of turtles in the UAV footage were calculated by measuring the straight carapace length (SCL) and straight carapace width (SCW) from images where the whole carapace was clearly visible. Measurements were conducted using ImageJ (Schneider et al. 2012) and UAV footage was calibrated using a transect of known length at 30 m altitude. In some cases, turtles could not be measured due to factors including turbidity, glare, depth, obstruction by overhangs or trees, partly obscured carapace, or obstruction of view of whole carapace due to dive angle.

To assess the L/W ratio of each species, calculate boundaries, and assign species to individuals, we used SCL and SCW measurements from immature hawksbill (< 60 cm SCL) and green turtles (< 65 cm SCL) captured in Turtle Cove between 1996 and 2021 and from green turtles captured in Seychelles (due to scarcity of green turtle captures in Turtle Cove) between 1981 and 2012. Green turtle carapaces were generally wider with a lower L/W ratio whilst hawksbill turtle carapaces were more elongated and had a higher L/W ratio. Turtles observed in the UAV footage were identified using these respective L/W ratios. To confirm numbers of hawksbill and green turtles in the population, we applied the ratio of hawksbill to green turtles identified (using the L/W measurements from live-captured turtles) to the total number of observed turtles in the UAV footage.

We assessed the abundance of hawksbill and green turtles live-captured between February to August 2021 to compare differences in the relative species abundance derived from live-capture versus UAV surveys.

Global immature hawksbill density review

A literature search was conducted in August 2020 and December 2021 for papers on Web of Science using the search term: ALL = ("Hawksbill turtle*" OR "*Eretmochelys imbricata*") AND ALL = ("Immature*" OR "Juvenile*") AND ALL = ("Abundance*" OR "Densit*" OR "Population estimate*" OR "Foraging site*" OR "Developmental site*"). We used Google Scholar to find all articles that had cited the first study to quantify hawksbills at a foraging site (Limpus 1992) and worked our way through each article (~173 results) for immature hawksbill density results. We checked all available Marine Turtle Newsletters (MTN) and International Sea Turtle Symposium (ISTS) proceedings for "Densit*" or "Abundance*" or "Population estimate*". Results using Catch Per Unit Effort were not included in our results. To compare hawksbill density results around the World, we calculated the mean and SD for sites that had included multiple density results for "zones" in close proximity and for studies over multiple years (e.g., Whiting et al. 2014). If a study had more than one estimate reported, then the mean was taken. If a site was reported in two separate studies, we chose the study that was the most recent and opted for an article (e.g., for Yucatan, Mexico; Cuevas et al. 2007). Data from Theses and symposium proceedings were not included in our results.

Data analysis

Density of turtles was calculated using total population counts and divided by the available area within each transect and calculated as number of turtles per square kilometre (turtles km^{-2}). Population density for each transect could then be used to calculate and extrapolate to the whole Turtle Cove area at different tidal heights of low, mid, and high water. The marking of white paint and satellite tag locations provided an opportunity for a mark-resight approach to calculate the population of immature sea turtles. We used the Chapman estimator (Chapman 1951) to calculate the abundance of immature turtles where:

$\hat{N}_c$ = population estimate

n_1 = number of marked turtles available to be resighted

n_2 = number of turtles observed from the UAV transects

m_2 = number of marked turtles resighted from the UAV transects

$$\hat{N}_C = \frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)} - 1$$

The abundance estimates from the Chapman estimator were divided by the area of Turtle Cove to calculate the number of turtles per square kilometre (turtles km^{-2}), which are the density results used in our study. Differences in perception bias (i.e., the ability to observe turtles in different conditions of glare, shade, etc) and availability bias (when animals present in the area were submerged and not visible due to turbidity, obstructions, overhangs, etc) (Marsh and Sinclair 1989) were accommodated within the CMR framework, since any perception or availability bias would equally impact the ability to see both marked and unmarked turtles. Likewise, we did not use any of the classic distance sampling approaches which assume that perception of objects decreases the further they are away from the ground track (Thomas et al. 2010).

To compare our results to global hawksbill density results, the average density was calculated from the available habitat area at low, mid, and high water which gave a range of densities at different tidal heights.

RESULTS

Physical captures

Length and width measurements were collected from 227 hawksbills and 35 green turtles from Turtle Cove between 1996 and 2021, supplemented with measurements from 88 green turtles from Seychelles. Most turtles captured in Turtle Cove were < 60 cm SCL (Fig. 7.3). Only 9% (15 out of 169) of all captured turtles in Turtle Cove between February and August 2021 exceeded this length and so were categorised as subadult or adult, of which two were males as indicated by the presence of a long tail. All hawksbill and green turtles captured in Turtle Cove since 1996 were < 81 cm and < 56.5 cm CCL respectively, while our measured range of sizes for nesting turtles of each species are 74.0-87.1 cm and 97.5-124 cm CCL, respectively.

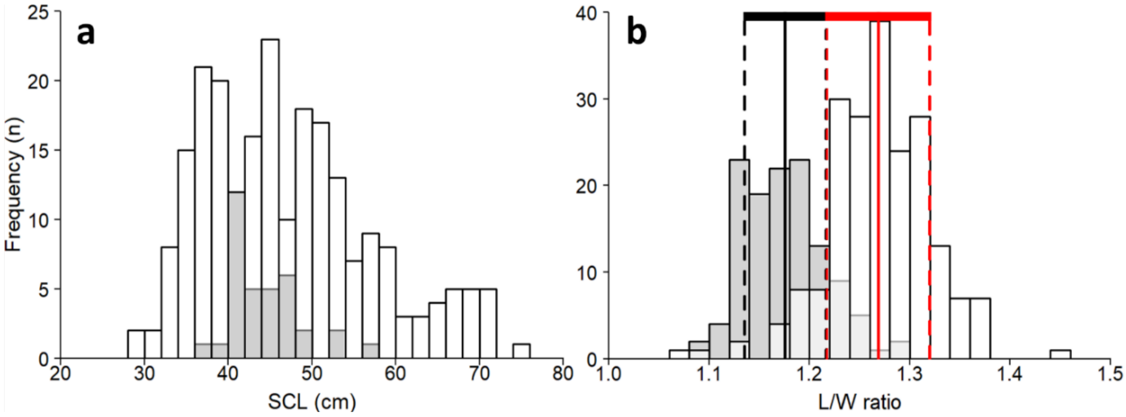

Figure 7.3. a) Range and frequency of hawksbill (white bars; *n* = 227) and green (grey bars; *n* = 35) turtle straight carapace lengths (SCL) for individuals captured in Turtle Cove (1996-2021). **b**) Frequency of length/width (L/W) ratios calculated from straight carapace lengths and widths for immature hawksbill (*n* = 201; < 60 cm SCL; white bars) and green turtles (*n* = 123; < 65 cm SCL; grey bars) in Turtle Cove (1996 - 2021) and Seychelles (1981 - 2012). For each species, mean L/W ratios are indicated by solid vertical lines, and standard deviation (SD) by dashed vertical lines (hawksbills = red; green turtles = black). The L/W ratios were used to inform species identification for turtles measured from Uncrewed Aerial Vehicle (UAV) imagery, with L/W ratio > 1.22 for hawksbills, and < 1.22 for green turtles.

Satellite tagging and marking turtles

High-resolution Fastloc-GPS satellite tags were attached to 27 immature sea turtles (25 hawksbills and 2 greens) between 2018 and 2021. Immature turtles showed high fidelity to Turtle Cove and during the 5-days after release, 85% of filtered Fastloc-GPS locations for the 27 turtles were within the Turtle Cove area (SD = 25.5%; Range = 19-100%; n of locations = 2888; Fig. 7.4). Over two days in February 2021, 50 immature turtles (48 hawksbills and 2 greens) were captured, marked, and released. Given the results from the satellite tracking, we estimated that 0.85 x 50 = 42.5 of the 50 turtles were available for resighting during the UAV surveys.

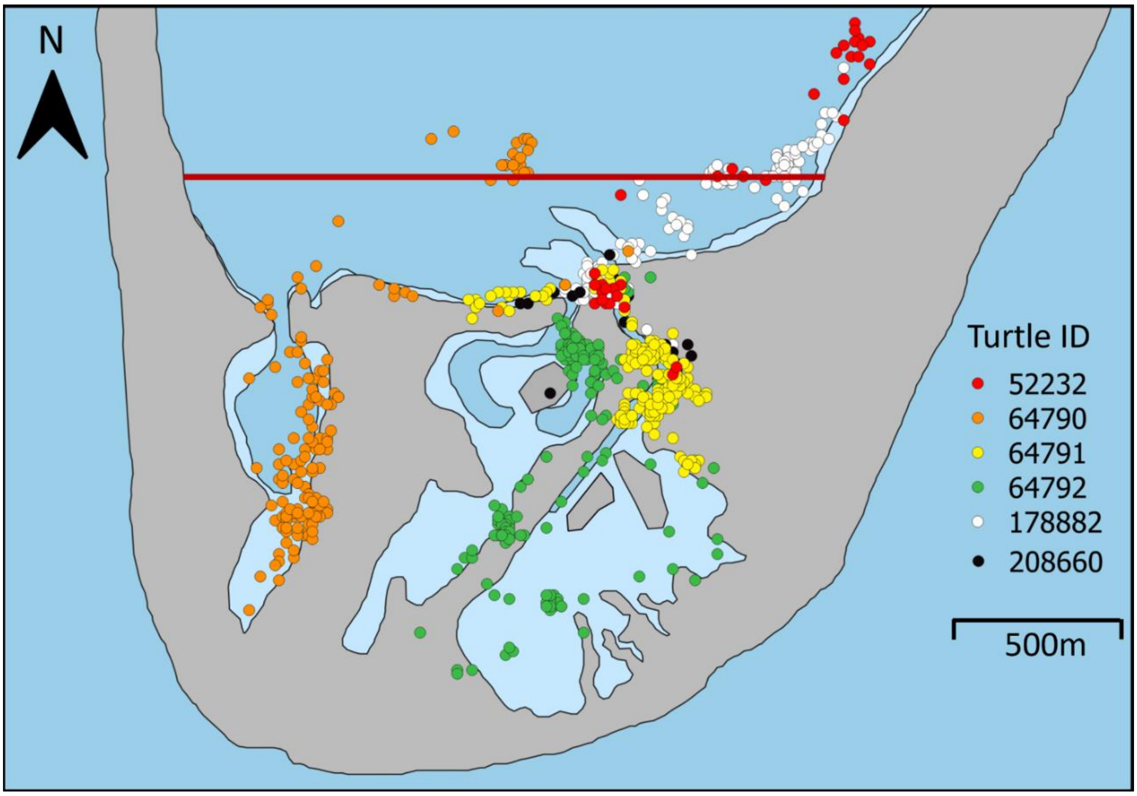

Figure 7.4. Filtered Fastloc-GPS locations after release (day 1 to 5) from six tracked immature turtles in 2018-2021, at Turtle Cove, Diego Garcia, Chagos Archipelago. Each coloured circle represents an individual Fastloc-GPS turtle location.

Species identification

The mean L/W ratio we calculated from captured turtles were 1.27 (SD = 0.05) for hawksbills, and 1.18 (SD = 0.04) for green turtles. For turtles that we were able to measure from clear UAV images (n = 67), those with a L/W > 1.22 we assigned as hawksbills, and those < 1.22 as green turtles (Fig. 7.3) and on that basis extrapolated the proportion of each species sighted in the UAV footage (n = 257). This L/W division assigned 203 as hawksbills. However, given the mean and SD in the measured L/W of hawksbills and assuming a normal distribution, 16% of hawksbills would be wrongly assigned as green turtles based on their L/W, i.e. would have a L/W of < 1.22. So, for example, if 100% of the 257 turtles were actually hawksbills then, on average, the L/W division would be expected to wrongly identify 41 turtles as green turtles. So, it is likely that the true proportion of hawksbill turtles is closer to (203 + 41) / 257 = 95%. Of 169 turtles physically captured at Turtle Cove between February and August 2021, 87% were hawksbills and 13% were green turtles. We therefore assumed that the true percentage of hawksbill turtles was mid-way between these two estimates from the UAV footage (95%) and from physical captures (87%), i.e., 91% of turtles were hawksbills.

Population estimation

UAV surveys in March 2021 totalled 23.2 km in length with a field of view width of 30 m and sea turtles were recorded on 257 occasions. Using the ratio of marked-to-unmarked turtles in the UAV footage, we estimated an abundance of 339 turtles (95% CI: 287-392) in Turtle Cove and population densities of between 265 turtles km^{-2} at high water and 499 turtles km^{-2} at low water. These are conservative estimates as we only included images categorised as “certain” turtles and did not consider those categorised as “potential” or “probable” turtles. The ratio of “potential or probable” to “certain” turtles in the footage was 5.97 (86% certain; 14% potential or probable). Given the proportion of hawksbill to green turtles derived from the L/W measurements, we therefore estimated densities at high and low water of between 241-454 turtles km^{-2} for hawksbills and 24-45 turtles km^{-2} for green turtles.

Review of immature hawksbill population densities

Our literature search located nine studies reporting immature hawksbill densities. Developmental habitat sites with density data included those in the Western Atlantic (mainly the Gulf of Mexico and Caribbean Sea, southern Indian Ocean (Mauritius and Cocos Keeling Islands) and one site in the Western Pacific (Heron Reef). Density estimates for hawksbill turtles at Turtle Cove were higher than all other densities recorded amongst comparable developmental habitats across the world (Fig. 7.5; Table S7.1), which ranged from < 0.01 to 201 turtles km^{-2}. The average density calculated from available habitat at low, mid, and high water tidal heights at Turtle Cove (343 hawksbill turtles km^{-2}) is greater than all other sites reported around the world.

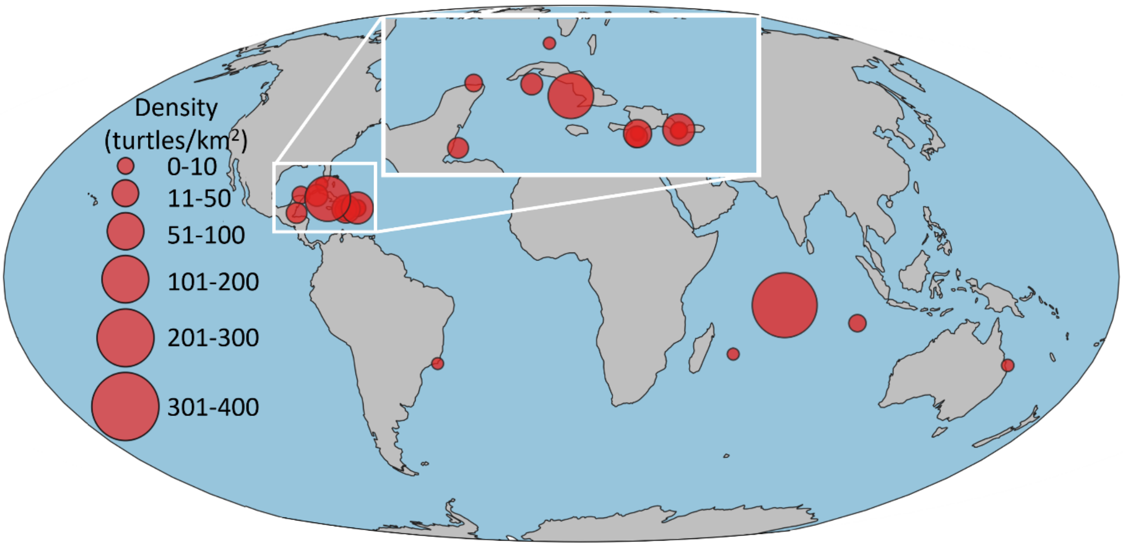

Figure 7.5. Juvenile hawksbill population densities (indicated by circle size) at development sites around the world (Source data: Appendix S1: Table S7.1). Where multiple densities were recorded for one site the mean density was calculated. [1] Key West, Florida; 1.8 turtles km^{-2}; Herren et al. 2018; [2] Rio Lagartos, Mexico; 34 turtles km^{-2}; Cuevas et al. 2007; [3] Doce Leguas, Cuba; 201 turtles km^{-2}; ROC 2000; [4] Isle of Youth, Cuba; 59 turtles km^{-2}; ROC 2000; [5] Playa Norte, Dominican Republic; 5.6 turtles km^{-2}; Leon and Diez 1999; [6] Bahia de las Aguilas, Dominican Republic; 6.6 turtles km^{-2}; Leon and Diez 1999; [7] Cabo Rojo, Dominican Republic; 8.2 turtles km^{-2}; Leon and Diez 1999; [8] Los Frailes, Dominican Republic; 58.3 turtles km^{-2}; Leon and Diez 1999; [9] Colita, Dominican Republic; 96.8 turtles km^{-2}; Leon and Diez 1999; [10] Mona Reef, Puerto Rico; 24.1 turtles km^{-2}; Diez and van Dam 2002; [11] Mona cliff wall, Puerto Rico; 28.6 turtles km^{-2}; Diez and van Dam 2002; [12] Monita cliff wall, Puerto Rico; 120 turtles km^{-2}; Diez and Dam 2002; [13] Glover's Reef, Belize; 53 turtles km^{-2}; Strindberg et al. 2016; [14] Arraial do Cabo, Brazil; 1e-10 turtles km^{-2}; Mello-Fonseca et al. 2021; [15] Mauritius; 0.49 turtles km^{-2}; Reyne et al. 2017; [16] Diego Garcia, Chagos Archipelago; 343 turtles km^{-2}; present study; [17] Cocos & Keeling; 32.5 turtles km^{-2}; Whiting et al. 2014; [18] Heron Reef, Australia; 3.3 turtles km^{-2}; Limpus 1992.

DISCUSSION

By combining UAV surveys, satellite tracking data and a mark-resight approach, we demonstrate how population abundance can be estimated and we revealed an exceptionally high density of foraging turtles. This synergistic use of approaches may have wide utility across a broad range of taxa. While UAVs are becoming a routine method for wildlife census surveys, species identification is not always straightforward. For example, Hensel et al. (2018), observed hawksbill and green turtles in the Bahamas and were not able to distinguish between these two sympatric species. Similarly, Kelaher et al. (2020), found difficulty in identifying between offshore bottlenose dolphins, (*Tursiops truncatus*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

To address issues with species identification, we developed an objective way of distinguishing species using morphological data based on their relative width versus length. This general approach of objective species identification might have wide applicability, especially where different species can be captured, and detailed morphometric measurements taken. The similarities in the proportions of each species recorded using both physical captures and UAV validates our species assignment and supports the use of L/W ratios in future studies that need to distinguish between sea turtle species. Further automated procedures for assessing morphology in UAV footage may have applicability such as the use of a Convolutional Neural Network (CNN) to detect whale species in UAV footage through morphological measurements (Gray et al. 2019) and machine learning algorithms to differentiate between shark species (Butcher et al. 2021). Our measurements of captured turtles revealed morphometric differences between two sympatric species and demonstrated that the foraging site is used primarily by small immature turtles. Notably all green turtles and most of the hawksbill turtles captured had smaller carapace length than adults measured whilst nesting at this study site.

Green turtles display an ontogenetic shift in diet towards herbivory at sizes greater than 30 cm CCL in benthic habitats (Burgett et al. 2018) and have a predominantly seagrass-based diet in the Western Indian Ocean (Stokes et al. 2019). For example, juvenile green turtles forage on animal matter in coastal habitats of southern Peru and then transition from a high to low calorie diet when they migrate north to feed on abundant vegetation (Quiñones et al. 2022). Given the lack of seagrass in Turtle Cove green turtles might not be expected to remain in this developmental habitat for extended periods. Very few adult hawksbills have been captured in Turtle Cove, which could be linked to the niche segregation between juvenile and adult hawksbill turtles, as seen at other sites such as Príncipe Island, West Africa (Ferreira et al. 2018).

The ability to detect animals from UAV footage can be heavily influenced by the type of background over which the UAV is flown. Often animals are a similar colour to their habitat and blend in with their surroundings. For example, Chabot and Bird (2012), found Snow Geese (*Chen caerulescens*) were easier to count as they stood out against their background compared to Canada Geese (*Branta canadensis*) which blended in. Most UAV surveys in the marine environment cover deeper, open water, and run into issues with sighting animals at depth (Bevan et al. 2016; Schofield et al. 2017b), although recent studies have found adjusting and accentuating the green colours in images during post-processing helps to detect submerged fauna (Colefax et al. 2021) in shallower water. Compared with other marine fauna such as dolphins, sharks and rays, turtles have a lower probability of detection and are more difficult to classify (Colefax et al. 2019). Conducting a UAV survey over a shallow, sheltered lagoon minimised these challenges to some degree as turtles were often visible resting on the seabed and wave action was minimal. However, in other turtle foraging habitats such as coral reefs, it is often more difficult (especially in rough sea or turbid conditions) to distinguish between turtles and rocky or reef structures. Likewise, in the terrestrial world, the meerkat (*Suricata suricatta*) can be easily confused with bushes or rocks (Rey et al. 2017). Therefore, we classed turtle sightings as ‘certain’, ‘probable’ and ‘possible’ and only included ‘certain’ sightings in our calculations leading to conservative estimates of turtle densities. Although machine learning algorithms are available, it is favourable to have a uniform background as increased habitat complexity has led to a decrease in detection rates, for example, detecting seals due to the presence of boulders of similar shape and size (Dujon et al. 2021). In cases of complex benthic or coastal habitats, perception and availability bias should be considered during analysis of aerial images (Fuentes et al. 2015).

Although our estimated ratios of species occurrence based on captures and UAV observations were very similar, in other cases UAV data may be biased to one species or another based on vigilance and escape reactions, or depth distribution, for example, missing animals or species at increased depths such as rays buried or animals under structures (McIvor et al. 2022). So, we recommend validation of UAV species identifications in multispecies assemblages, as we have done using in-water captures at the same site. Similarly, it is well known there may be sampling biases with studies across multiple taxa. For example, slowly towed plankton nets will tend to underestimate the abundance of faster moving plankton such as fish larvae (Thayer et al. 1983) and traps often selectively catch certain species (Harvey et al. 2012). Our approach and findings show how UAV surveys, when combined with capture data may inform future studies of foraging turtles where major knowledge gaps exist across species (Hamann et al. 2010).

Population estimates from CMR studies are often based on assumptions of immigration and emigration. Closed population models assume births, deaths, immigration, and emigration are not occurring (Dail and Madsen 2011), whilst these assumptions are relaxed in different ways for open population models (Kendall and Bjorkland 2001). Often these assumptions are ignored or not met (Pollock 1991). It is important to know what proportion of marked individuals remain in the study area and so are available to be re-counted in the recapture/resights. While UAVs have been used in combination with a mark-resight approach to estimate nesting turtle abundance (Dunstan et al. 2020), the added value of satellite tracking individuals to assess emigration rates has not been considered. Both UAV and tracking studies are now increasingly used across various wildlife species including sea turtles (Hays and Hawkes 2018; Schofield et al. 2019) and we have shown the added benefit of performing both these types of study at the same site, with the tracking data enhancing the value of UAV surveys. Our finding that in the five days after release most turtles remained within the locality of the capture site accords with detailed movement analysis showing generally very small home ranges for immature turtles in the Chagos Archipelago (Hays et al. 2021a). Given this benefit of knowing the proportion of marked individuals available for recapture or resighting, we advocate this use of animal tracking within mark-resighting UAV surveys across taxa and not only for sea turtle studies.

Our findings show immature hawksbill turtle densities at Turtle Cove to be higher than those reported at hawksbill developmental sites elsewhere in the world. Despite the circum-tropical distribution of hawksbill turtles (Mortimer and Donnelly 2008), relatively few estimates of turtle density on their foraging grounds have been calculated, likely reflecting the inherent difficulties of obtaining these density estimates, but this is likely to change given the increased use of UAV surveys. For immature turtles, reported density estimates vary widely from < 0.01 turtles km^{-2} in Brazil (Mello-Fonseca et al. 2021) to 201 turtles km^{-2} in Cuba (ROC 2000). This wide variation in density might reflect several factors such as the proximity of large nesting populations that provide a source of juveniles, the varying suitability of different habitats or the extent of long-term protection. The importance of long-term protection is implicated in the results from Doce Leguas, Cuba with a mean hawksbill density of 201 turtles km^{-2}, where all marine turtles have been protected since 1995 and traditional harvesting by local communities is controlled and regulated (ROC 2000). Our findings provide further evidence that long-term protection has helped drive high densities of turtles at some foraging sites (e.g., the recovery of green turtles in the Hawaiian Archipelago; Balazs and Chaloupka 2004), given that Turtle Cove has been well protected for several decades (Sheppard et al. 2012). The human population on Diego Garcia is relatively small (usually less than 2000 people), prohibition of people entering the water at Turtle Cove is supported by regular enforcement patrols and severe fines for any unauthorised activity in the water. Our data provide evidence that restricted military sites often support high biodiversity due to the exclusion of the general population and a reduction in certain anthropogenic impacts (Zentelis and Lindenmayer 2015). Human activity in restricted military areas is typically strictly controlled with little or no disturbance over long periods. Another example is that of Donna Nook in the Humber estuary, a military site used as a weapon and bombing range, where grey seal pups have increased in number from around 30 to almost 2,000 between 1984 and 2016 (Russell et al. 2019).

Broader ecological consequences of the high densities of foraging hawksbills that we report might be expected. Experimental studies in Indonesian seagrass meadows have shown that increased rates of grazing by green turtles may increase primary productivity and biomass as well as potentially increase tolerance to high nutrient loads (Christianen et al. 2011). On the other hand, high densities of foraging green turtles have been linked to overgrazing of seagrass meadows at sites in Bermuda, North Atlantic

(Fourqurean et al. 2010), Great Barrier Reef, Australia (Scott et al. 2020) and the Lakshadweep archipelago, Indian Ocean (Gangal et al. 2021). Turtle body condition is likely to deteriorate in habitats that they have overgrazed, but the links between hawksbill turtle foraging density, grazing impacts and body condition are yet to be identified.

Marine protected areas (MPAs) can help protect biodiversity (Sala and Giakoumi 2018), and Diego Garcia lies at the heart of one of the world's largest MPAs, with the benefits of minimal anthropogenic impacts extending to fish stocks, coral reef health and seabird abundance (Hays et al. 2020). We have previously shown that the numbers of nesting hawksbill and green turtles are increasing (Mortimer et al. 2020). Our findings presented here that Turtle Cove on Diego Garcia supports the highest density of foraging hawksbill turtles ever reported provide further evidence of the value of long-term protection of developmental habitats.

ACKNOWLEDGEMENTS

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CHAPTER EIGHT: Assessing the impact of satellite tagging on growth rates of immature sea turtles

This work has been submitted to Methods Ecol Evol as:

Stokes HJ, Stokes KL, Mortimer JA, Laloë J-O, Esteban N, Hays GC. Assessing the impact of satellite tagging on growth rates of immature sea turtles.

Disclaimer: GCH, NE and HJS conceived the study. GCH, NE, JAM, J-OL, and HJS completed the fieldwork. HJS collated the data and calculated growth rates. HJS, KLS, GCH, and NE conducted statistical analysis. HJS and GCH led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

ABSTRACT

Animal-borne devices including transmitters, data loggers and identification tags, are widely used across taxa to address important biological and ecological questions. However, these devices may affect fitness, hence studies to assess device impacts are important across taxa and developmental stages. We assessed the long-term effects of satellite tagging on sea turtles at a foraging site in the Indian Ocean. Hawksbill turtles (*Eretmochelys imbricata*) were captured between 2018-2023, and satellite tags (Fastloc-GPS Argos) were attached to 25 individuals between 2018-2021, with a mean Straight Carapace Length (SCLn-t) of 55.3 cm (SD = 6.9; range = 47.9-69.5 cm; n = 21). We recaptured 12 tagged turtles and removed 11 tags between 2021-2023 and estimated growth rates of tagged (n = 10) and untagged (n = 44) animals (mean SCL range = 33.3-69.4 cm) using capture-mark-recapture of 54 individuals at liberty for 730-1095 days. Growth rates decreased exponentially as turtle size increased, and we found no significant difference between tagged and untagged growth rates and body condition. We also found no damage to the carapace from the tag attachment. We speculate that tagging does not influence growth rates at this study site because the turtles (i) move little and (ii) feed on benthic forage, not actively pursuing prey. We encourage best practice to study the long-term effects of satellite tagging on turtle populations around the world, as the outlook may be different for animals that swim long distances and/or carry large devices.

KEYWORDS

animal welfare, conservation, critically endangered, marine megafauna, Marine Protected Area (MPA), tracking

INTRODUCTION

Understanding animal behaviour, movement and distribution is essential for successful conservation and management planning (Hays et al. 2019). With the rise in reliable satellite tracking technology and associated streamlined animal-borne data loggers, many challenges have been overcome associated with studying marine animals that span large spatio-temporal scales across dynamic oceans (Hart and Hyrenbach 2009). Many marine animals are routinely tracked using satellite technology, including birds (e.g., penguins, albatrosses), fish (e.g., sharks, rays), mammals (e.g., seals, whales) and reptiles (e.g., sea turtles) (Hussey et al. 2015). Satellite tracking provides information on animal movements as well as detailed behavioural information such as diving behaviour (Luschi et al. 2013), speeds of travel and environmental conditions (e.g., sea temperature) (Hussey et al. 2015). Satellite tracking data have been used widely in conservation management such as in the design of marine protected areas (MPA) (Dawson et al. 2017), informing fisheries management (Hussey et al. 2017), and reducing vessel strikes (Shimada et al. 2017).

Attachment methods vary between animals, species, and life stages, such that a harness-attached tag might be preferential for some birds (small and medium-sized birds; Jirinec et al. 2021), while epoxy attached directly to the carapace is the typical method for adult hard-shelled sea turtles (Hays and Hawkes 2018). The aim of animal-borne data loggers is to optimise data collection whilst minimising adverse effects to the animal, and although studies have shown no effect of satellite tagging (Sergio et al. 2015) tag attachment in many cases can influence the exact data sought from these devices, including movement and behaviour. Further, the position of the device has been associated with effects on survival and reproduction (Bodey et al. 2017). Care is needed to reduce the potential impacts of tagging. Nevertheless, negative effects have been reported on animal movement (e.g., pop-up satellite tags increase drag of the European eel, *Anguilla anguilla*, Methling et al. 2011), behaviour (e.g., changes in diving behaviour of great cormorants, *Phalacrocorax carbo*, Vandenabeele et al. 2015), survival (e.g., pop-up satellite tagging injury on shortnose sturgeons, *Acipenser brevirostrum*, Broell et al. 2016), and growth (e.g., Atlantic salmon *Salmo salar* growth reductions likely due to drag, Hedger et al. 2017).

Often with tagged animals there may be little to no opportunity to observe if a device attachment has caused detrimental effects to the animal, as the animal may not be recaptured after release, such as in many satellite tracking studies with fish and sea turtles. Furthermore, while short-term deployments, for example of data-loggers, may have little influence, often over very long deployments negative effects may increase. For example, in a seminal study it was shown that simple, non-electronic, flipper bands used to identify individuals caused increased mortality of penguins, likely through long-term (e.g., over 10 years) effects of increased drag leading to loss of fitness (Saraux et al. 2011).

Here we take advantage of the generally long-term fidelity of juvenile sea turtles to a foraging ground in the Indian Ocean (Hays et al. 2021a) to assess long-term effects of satellite tag attachment. Further we assess if attachment caused any long-term physical damage to the carapace. We highlight the importance of these types of studies to assess the effects of tagging on different species and developmental stages around the world and hence to encourage best practices.

MATERIALS AND METHODS

Capture-mark-recapture

Immature hawksbill turtles were captured as part of a long-term in-water sampling program in Turtle Cove, Diego Garcia (7.428° S, 72.458° E; Fig. 8.1a). We waded in shallow water (<0.5 m) and quietly approached and captured turtles from behind whilst they were feeding. Turtles were brought to the beach to conduct carapace size measurements and flipper tagging. At first encounter, turtles were flipper-tagged on both front flippers using Inconel (National Band and Tag Company, KY, USA) tags, and biometric measurements were taken at initial capture and recapture, including curved carapace length notch-to-tip (CCLn-t, hereafter CCL; Bolten 1999), straight carapace length notch-to-tip (SCLn-t, hereafter SCL; Bolten 1999), using vernier callipers and weight (using a spring balance). Mean mass divided by mean SCL cubed was used as a metric for body condition (mass/SCL^3).

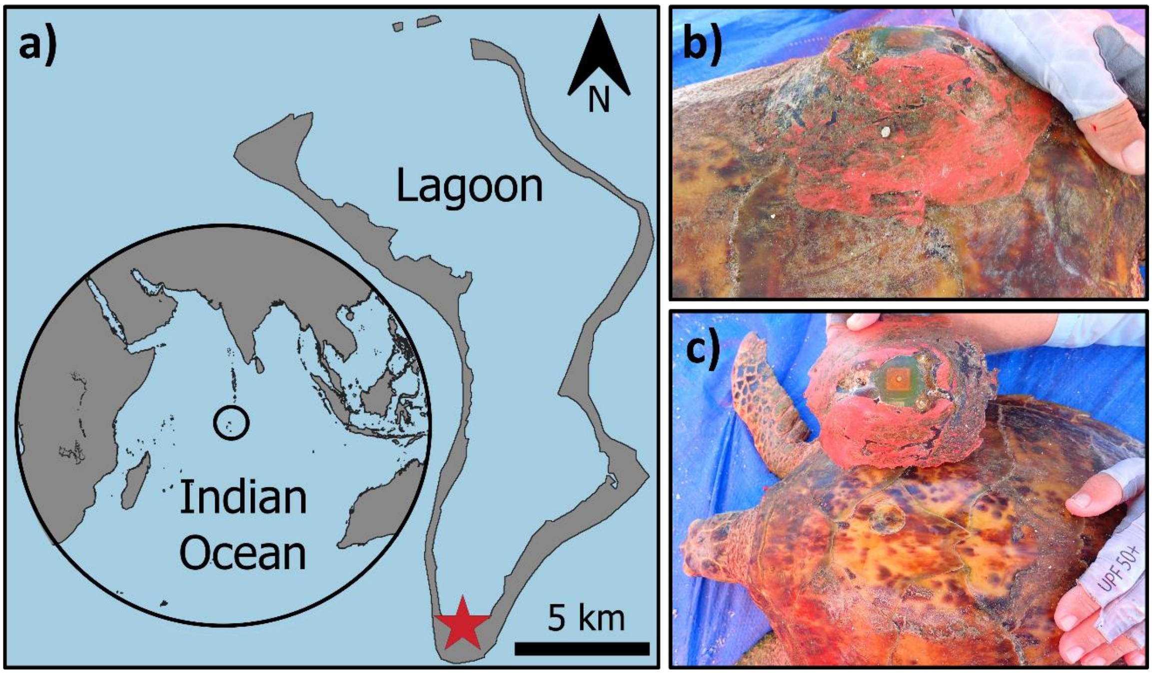

Figure 8.1. a) Diego Garcia with an inset map showing the location of the Chagos Archipelago (black circle) in relation to the wider Indian Ocean. The red star indicates where the hawksbill turtles were captured and equipped with a satellite tag (Fastloc-GPS Argos transmitter) at the south of the lagoon (Turtle Cove). **b)** example of a

satellite tag 3 years post attachment and **c)** an example of a hawksbill turtle carapace post satellite tag removal showing no signs of damage.

Satellite tagging

Satellite tags with Fastloc-GPS (SPLASH10-BF-297B-01, Wildlife Computers, Seattle, Washington, USA) were attached to 25 hawksbill turtles between 2018 and 2021 (for detailed attachment methods see Hays and Hawkes 2018). Length x width x height dimensions of the tags were 86 x 55 x 26 mm and their weight in air 130 g. Satellite tags were only attached to individuals with a CCLn-t >50 cm (mean CCL = 60.2 cm, SD = 7.5; range = 51.1-74.5 cm; n = 25; mean SCL 55.3 cm, SD = 6.9; range = 47.9–69.5 cm; n = 21) and the weight of these turtles was generally >15 kg. As immature turtles in Diego Garcia generally show high fidelity to their foraging grounds (Hays et al. 2021a), recaptures of the same individuals are frequent. We recaptured 12 turtles post satellite tagging and removed 11 tags between 2021 and 2023. Tags were removed if there were signs of detachment from the carapace, for example, the epoxy was weak along the edges and the tag and epoxy could easily be prised off the carapace. Tags were not removed if they were fully secure to the turtle (n = 1). To compare tagged and untagged individuals we filtered the data to reflect tagged turtle recapture intervals, and so turtles were only included if recaptures occurred between 730-1095 days. We plotted growth rates against SCLn-t rather than CCLn-t, as we more frequently had SCLn-t measurements at both capture and recapture (n = 10).

Growth rates

Growth rate (cm/yr) was calculated for each turtle using SCLn-t:

$[SCL_{(re\text{-}capture)} – SCL_{(capture)}]$ / recapture interval in years.

Mean SCLn-t (cm) was calculated by taking the mean of the initial and recapture SCL measurements. For growth rate analysis and the relationship between mass and SCL, outliers were identified and removed after plotting CCL against SCL when residual values from the positive linear relationship were > 2 cm (9 out of 310 points; Fig. S8.1), likely as a result of a mismeasurement or an error in transcription. The linear relationship between SCL and CCL was explored only using initial capture measurements from each individual (n = 196; Fig S7.1). For growth rate analysis and the relationship between mass and SCL, we set lower and upper limit intervals (730-1095 days) between capture and recapture. Short intervals can increase sample size greatly, but measurement error can then dramatically alter estimated growth rate, particularly for slow growing populations. On the other hand, including very long intervals between measurements increases the risk of missing size-specific growth rates. Negative values which could be down to measurement error or deterioration of the carapace (Bell and Pike 2012) were not excluded from this dataset to avoid bias. We also removed repeated measurements from the same individuals. The most recent measurements were retained unless the measurement removed was from an individual equipped with a satellite and if so, preference was given to measurements from satellite tagged individuals.

Statistical analyses

We conducted a Pearson product-moment correlation test and fitted a quadratic model to examine the relationship between mean SCL and mean mass. All growth rates were increased by a value of 1 to transform negative values (n = 2) into positive ones in order to fit the growth rate model with an exponential decay formula using log-growth rates. The relationship between growth rate, SCL and satellite tag attachment was explored using linear modelling with growth rate as the response variable, and SCL and tagged/untagged as fixed effects. Model comparison was performed using maximum likelihood estimates, and model residuals were checked for homoscedasticity and normality. T-tests were also conducted to explore if there was a significant difference in growth rates or body condition (mass/SCL^3) of individuals with and without a satellite tag between 50-60 cm SCL. All plots were created, and statistical analyses were performed in R (R Core Team; version 4.2.2).

RESULTS

Capture-mark-recapture

Between 2018 and 2023, we captured 199 individual hawksbill turtles on 331 occasions in Turtle Cove, Diego Garcia. Green turtles were also captured at this site but there were no recaptures. From these 331 captures, hawksbill turtles ranged from 30.5 cm CCL, 28.8 cm SCL and 2.5 kg at initial capture to 76.0 cm CCL, 70.3 cm SCL and 36.7 kg at recapture (Fig. S8.1). After removing recaptures that occurred outside 730 - 1095 days, and repeated measurements from the same individuals, we obtained 54 growth rates that were on average 918 days apart (SD = 79 days, range 736-1066 days). The remaining 54 individuals mean SCL ranged from 33.3-69.4 cm. As expected, turtle SCL and CCL have a strong linear relationship (SCLn-t = 0.978 + 0.918*CCLn-t; $r^2 = 0.99$; n = 196; $F_{1,194} = 26370$; $P < 0.001$; Fig. S8.1), and turtle mass increased significantly with SCL (Mass = 11.7 -0.73*SCL + 0.02*SCL^2; $r^2 = 0.98$; n = 54; $F_{2,51} = 1338$; $P < 0.001$; Fig. 8.2).

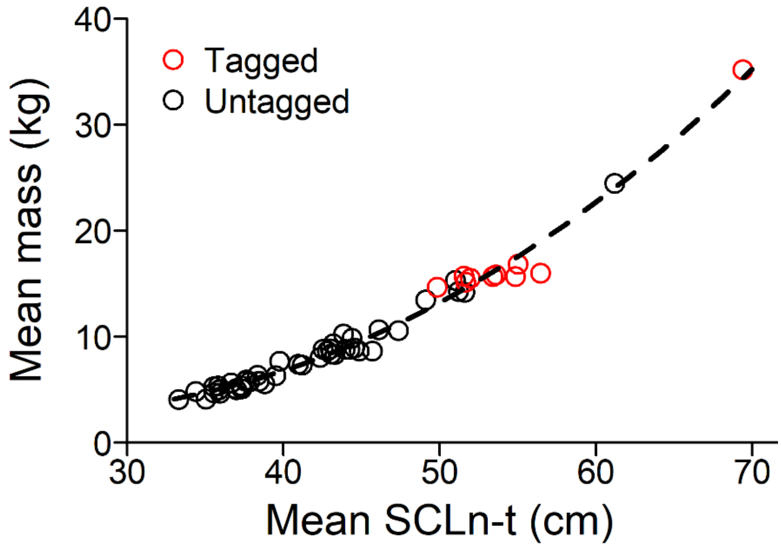

Figure 8.2. Mean mass of individual juvenile hawksbill turtles versus their mean straight carapace length (SCLn-t). The mean for each individual was calculated from the initial and recapture measurements. Black dashed line shows a fitted quadratic model (Mass = 11.7 -0.73*SCL + 0.02*SCL^2; $r^2 = 0.98$; n = 54; $F_{2,51} = 1338$; $P < 0.001$).

Satellite tagging

We examined the carapaces of 11 hawksbill turtles post satellite tag removal, after 2–3 years of attachment. On removal, we found no direct damage to the carapace, including no significant scute damage on the edges untoward of regular occurring damage and no significant thinning of keratin. Turtles in the cove are regularly found with algal build up on their carapace and this can be seen built up around the tag (Fig. 8.1c).

Hawksbill turtles grew on average 1.2 cm per year (SD = 0.7 cm; range -0.5–2.9cm; n = 54; Fig. 8.2). Growth rate decreased exponentially as mean carapace size increased (growth rate = 9.1192*exp(-0.0339*SCL) -1; $r^2 = 0.44$; n = 54; $F_{1,52} = 40.91$; $P < 0.001$; Fig. 8.3). For example, between 33.3 and 39.9 cm mean SCL, mean growth rate was 1.57 cm per year, whilst turtles between 50.0 and 59.9 cm grew on average 0.54 cm per year (Fig. 8.2). We found no significant relationship between mass gain and mean SCL (Fig. S8.2).

The 54 growth rates included 10 turtles with satellite tags. The tagged turtles were on average 54.8 cm mean SCL (SD = 5.5 cm; range 49.9-69.4 cm) and tagged turtle growth rates ranged between -0.5 to 1.12 cm per year. There was no significant effect of tagging when comparing growth rate models with and without an extra term describing which individuals were tagged ($F_{52,51} = 0.79$; $P = 0.38$), suggesting that tagging did not influence turtle growth rates (Fig. 8.3). We also compared tagged (n = 8) with untagged individuals (n = 3) measuring 50-60 cm SCL (i.e., the size range that included most of the tagged turtles) and found no significant difference between the growth rates of tagged (mean = 0.5 cm/yr) and untagged (mean = 0.8 cm/yr) hawksbill turtles ($t_4 = 1.05$; $P = 0.35$). Between 50-60 cm SCL, there was also no significant difference in the body condition of recaptured satellite tagged turtles and unequipped turtles ($t_5 = 1.05$; $P = 0.34$).

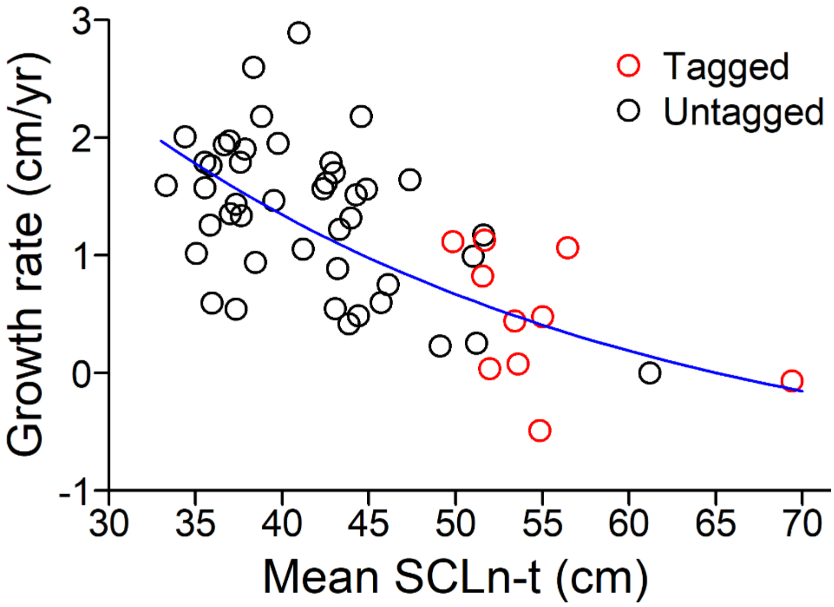

Figure 8.3. Relationship between mean straight carapace length (SCLn-t) and growth rate. Growth rate decays exponentially with turtle size (linear model: blue line) for tagged (red circles) and untagged (black circles) juvenile hawksbill sea turtles (growth rate = 9.1192*exp(-0.0339*SCL) -1; r^2 = 0.44; n = 54; $F_{1,52}$ = 40.91; $P < 0.001$).

DISCUSSION

For immature hawksbill turtles, we found no significant effect from satellite tagging on growth rates. Both tagged and untagged individuals grew at similar rates. Nor did we find that long-term attachment (several years) physically damaged the carapace.

Our findings are encouraging and suggest that satellite tracking can provide long-term behavioural data from small turtles (>50 cm CCL), without affecting their fitness. Several elegant studies with animals, or models of animals, in wind tunnels to address device impacts (Jones et al. 2013; Vandenabeele et al. 2015; Watson and Granger 1998) have shown that energy expenditure increases with the physical size of a tag in response to drag (e.g., the cross-sectional area) and weight. Since the effect on drag scales with the speed of travel, maximum tag effects are expected for larger devices deployed on small, fast-moving animals. Studies of how devices effect free-living animals complement these drag and energy expenditure calculations from laboratory studies. For example, long-term increases in mortality in penguins from flipper banding can be linked to the relatively small size of penguins and their fast-swimming speeds and hence even a small attachment can have serious negative effects (Saraux et al. 2011). In contrast, the juvenile turtles that we equipped travel little, generally maintaining small home-ranges (Hays et al. 2021a), and they graze on benthic animals and plants and so do not need to swim fast to capture prey. The combination of minimal movement and slow swim speeds likely helps explain the lack of device impact that we recorded and helps explain why wind tunnel studies have suggested that while most external tags likely cause minimal drag to adults, larger devices might sometimes cause significant increased drag for juveniles when swimming quickly (Jones et al. 2013; Watson and Granger 1998).

In the case of bird tagging studies, a 5% rule is generally followed, whereby the mass of the tag should be less than 5% of the bird's body mass (Wilson et al. 2002) and this has followed through into tagging studies of other terrestrial and marine organisms. However, although this concept reduces the effect of tags on flying birds, for some marine animals the mass of the tag may be less important due to buoyancy control. Sea turtle buoyancy is regulated by the volume of air inspired in their lungs (Hays et al. 2004) and, since turtles adjust this volume to achieve the desired level of buoyancy on the bottom phase of dives, it is likely that they can alter their lung volume to compensate for the extra mass of the tag. Similarly, the buoyancy of some marine mammals varies within a dive, for example due to lung compression with depth, and also with their body condition (e.g., Richard et al. 2014). So here again with marine mammals, the weight of the tag may simply lead to compensatory adjustments with buoyancy control.

As well as increasing drag, tag attachment can negatively affect free-living animals in a number of other ways. For example, in some cases the attachment itself may cause trauma at the point of contact, such as when darts are used to secure tethered tags to marine mammals (e.g., Andrews et al. 2019). In this regard it is reassuring that we found no long-term impacts of the attachment to the turtles' carapace. The situation may be different with soft-shelled turtles, such as leatherbacks (*Dermochelys coriacea*) and flatbacks (*Natator depressus*), where harnesses have been used that can cause abrasions, for example, to the hind flippers in flatbacks (Sperling and Guinea 2004). Indeed, this concern with abrasion from harnesses led to the development of a method of directly attaching satellite tags that is now used as best-practice for leatherback turtle satellite tracking (Fossette et al. 2008).

Another negative effect of tagging is that tags might sometimes act as lures and increase the risk of predation for tagged animals. This influence has been noted, for example, with fish carrying tethered pop-off tags. For example, from the tag data, migrating eels have been observed being consumed, presumably by large predatory fish or by marine mammals (Koster et al. 2021). The juvenile hawksbill turtles that we tagged live in a shallow lagoonal habitat, lacking large sharks, making this a relatively safe foraging environment (Stokes et al. 2023a). Moreover, the tags we deployed are not tethered, further minimising the risk of predation for this population.

Tracking studies involving a range of marine animals have provided valuable information that has helped drive conservation planning and ultimately enhanced the conservation status of a range of species, including fish, mammals, birds and sea turtles (Hays et al. 2019). While animal tracking clearly has great merit, we echo the view of Walker et al. (2011) and Batsleer et al. (2020) who encourage practitioners to publish evidence of tagging impacts for each study species, environmental conditions, and tag type regardless of whether they found no or little impact and, in this way, develop and refine best practices based on empirical evidence.

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CHAPTER NINE: General discussion

The overarching aim of this thesis was to further our understanding of sea turtle ecology, particularly nesting ecology which has largely been understudied due to the remoteness of the Chago Archipelago. Although nesting ecology was the focus, the thesis aims changed to adjust for the impact of the pandemic and delays to the initial expedition. The thesis starts broad with a global review of green turtle diet, moving onto green turtle nesting ecology in the Chagos Archipelago, and how traditional surveys and modern technology (remote and *in situ* sensing) can be combined to increase temporal and spatial coverage to increase our understanding of sea turtle ecology across all life stages in the remote islands of the Chagos Archipelago (Fig. 9.1).

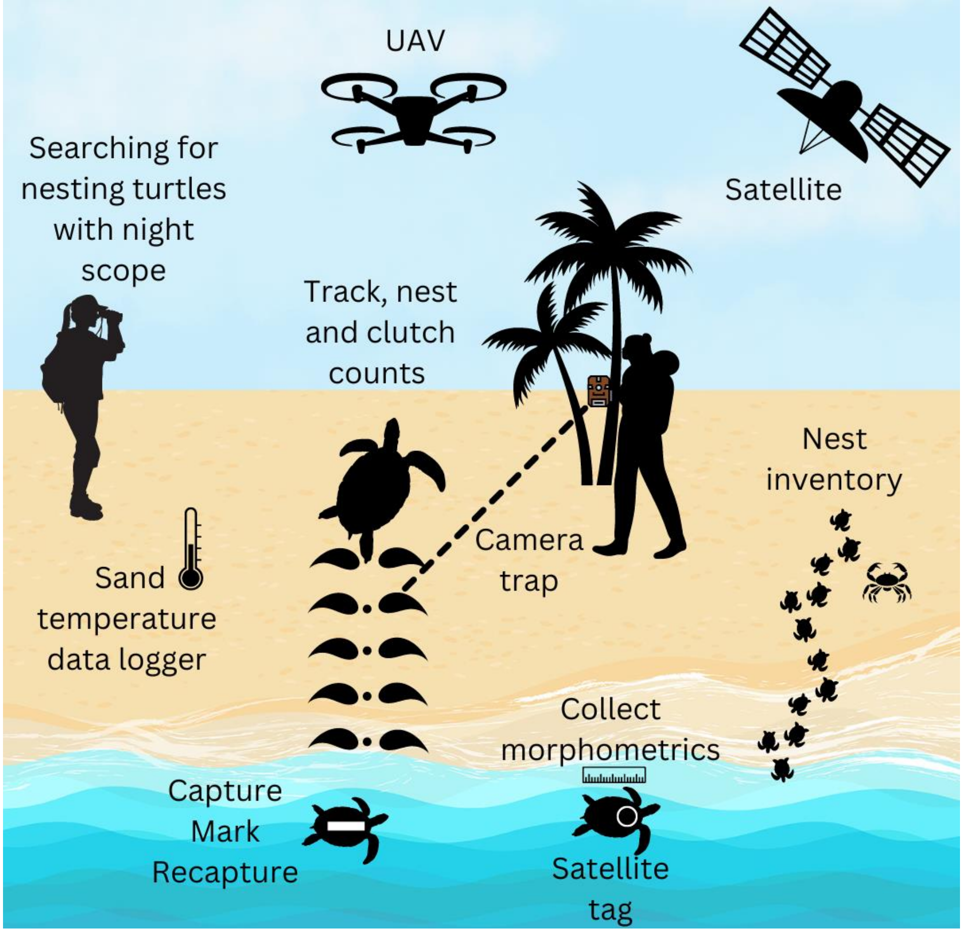

Figure 9.1. Combination of methods, including traditional ground surveys and remote and *in situ* sensing techniques, used to survey and monitor sea turtles in the Chagos Archipelago.

Initial efforts were focussed on global green turtle diet and the review revealed that green turtle diet varied around the world. We report that temperature may be an important driver of omnivory as diet was generally herbivorous at warmer sites yet omnivorous with higher levels of animal matter in areas at high latitude sites or cold-water currents (Chapter 2; Esteban et al. 2020). Although true for many sites where adult green turtle diet is primarily herbivorous and dominated by seagrass (Bjorndal 1980; Mortimer 1981), these findings were commonly reported for adult green turtles globally for which we found the opposite.

The next chapters were based on data collection to understand nesting ecology of green turtles, particularly threats to reproductive success (Chapter 3, 4, and 5). The first chapter investigating reproductive success of green turtles in the Chagos Archipelago explored nest site selection (chapter 3). To address this knowledge gap about green turtle nest site selection in the archipelago, nighttime surveys were conducted on the index beach in Diego Garcia, to observe nesting females and record their nest locations in relation to vegetation, the sea, and the high-water line. We found the majority of green turtles nested under vegetation (90%) and from a review of nest site selection of all species around the world, we concluded that turtles generally tend to crawl an adequate distance to minimise over-wash of nests and potential inundation to increase embryo survival. We highlight that embryo survival seems to be the key consideration in where sea turtles nest over hatchling sex ratios (Stokes et al. 2024).

Where a sea turtle decides to nest determines overall incubation conditions and so the following chapter (chapter 4) explored the spatial and temporal variability in sand temperatures across the Chagos Archipelago. In order to do so, temperature loggers were buried in the sand and spot measurements using a temperature probe were conducted in different nesting habitats, and sites along nesting beach on islands across the Chagos Archipelago. We expanded on the study by Esteban et al. (2016) with a decade-long dataset and found the main drivers of thermal variability were seasonal and interannual differences although both intra- and inter-beach further altered sand temperatures. Mean monthly sand temperatures were relatively low and we were able to show a wide range of temperatures at this nesting site which suggests both male and female-biased clutches are produced across the nesting season (Chapter 4).

Another factor that can influence offspring survival is predation risk to sea turtle eggs. From opportunistic observations, clutch counts, and nest excavations we were able to highlight key predators of green turtle eggs in the Chagos Archipelago and assess the number of eggs predated within the nest and how many eggs were removed from the nest. We report the first published observations of native coconut crab and invasive rat predation of sea turtle eggs around the world (Chapter 5; Stokes et al. 2023b). This study could be expanded further to understand predation rates from each type of predator and to establish where on the nesting beaches and when over the incubation period and nesting season are sea turtle eggs in the Chagos Archipelago most vulnerable to predation.

As long-term changes in offspring survival can influence population trajectories (Reichert et al. 2020; Parker et al. 2021), it is important to collect accurate temporal and spatial data of sea turtle tracks and nests to calculate estimates and assess trends. Increasing effort temporally is difficult at remote locations and so in this thesis camera traps were trialled to count tracks on the index beach in Diego Garcia. We demonstrated how camera traps can be used for track longevity estimates and track counts by validating our results with foot patrol surveys. Camera traps can increase temporal coverage at remote sites and help detect shifts in nesting seasons as a potential result of climate warming and interannual variability to assess trends. From running simulations, we found that the camera trap design can be altered to suit the length and density of tracks for application on nesting beaches around the world. Our results show the importance of conducting foot patrol surveys for detailed nesting data, but we believe traditional surveys can be combined with *in situ* and remote sensing such as aerial surveys (plane, UAV, satellite imagery) to increase spatial coverage and camera traps to increase temporal coverage as complimentary tools to increase confidence in estimates and trends (Chapter 6).

As we discussed the use of sensing technology for nesting populations in the previous chapter (Chapter 6), in chapter 7 a combination of UAV surveys, satellite tracking data, and mark-recapture was used to estimate abundance of immature turtles. To conduct this research, day surveys were undertaken at Turtle Cove, Diego Garcia. Immature turtles were captured, measured, marked and released. UAV flights were conducted five days later to count marked and unmarked turtles to calculate the abundance of immature turtles at an important foraging and developmental habitat. We demonstrated how the combination of these methods can be used for population densities and abundance estimates and developed an objective way to distinguish between hawksbill and green turtles using morphological data based on their length-to-width ratios (L/W). We found similarities in the proportion of each species recorded from physical captures and UAV images which validated our species assignment and the use of L/W ratios in future studies. We revealed an exceptionally high density estimate of immature hawksbill turtles at Turtle Cove and to place these results in a broader context, immature hawksbill turtle densities were collated from published results at other comparable sites. The density of immature hawksbill turtles at Turtle Cove were higher than any other population recorded around the world (Chapter 7; Stokes et al. 2023a).

The final study (Chapter 8) investigated the impact of satellite tagging immature turtles after the opportunity presented itself to remove satellite tags from turtles during data collection for chapter 7. Turtles were measured pre- and post-tagging and the attachment site of the tag after removal was assessed for damage. For this chapter, growth rates were compared between tagged and untagged individuals and the carapace condition was assessed. No significant difference in growth rates and no damage to the carapace from tag attachment was found. However, we speculate that tagging may have little effect on the turtles at Turtle Cove as they move little and feed in shallow waters on benthic food sources rather than actively pursuing prey. Therefore, we encourage best practice and highlight the importance of studying long-term effects of satellite tags on different turtle populations that swim long distances or carry large devices (Chapter 8).

Policy and Management

International policy for sea turtle protection in the Chagos Archipelago includes a Ramsar Site on the east of Diego Garcia. This site provides full protection for green and hawksbill turtles nesting and foraging on oceanside and foraging at Turtle Cove in the south of Diego Garcia lagoon (Convention on Wetlands of International Importance; RAMSAR). The UK is a party state to CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) since 1976 of which green and hawksbill turtles are listed under Appendix 1, to the Bonn Convention on Migratory Species (1979) and related Memorandum of Understanding for the Management of Sea Turtles within the Indian Ocean and Southeast Asian Region (IOSEA). All of which commit to conserving and restoring habitat, reducing activities that effect migration and prohibiting the taking of listed species. Locally, green and hawksbill turtles have been protected by conservation legislation in the Chagos Archipelago since 1968 and 1970, respectively. The Diego Garcia Conservation (Restricted Area, Fig. 9.2) Ordinance 1994 prohibits access to environmentally sensitive areas unless a permit has been approved and recreational fishing or any activities that could potentially be damaging are also not permitted in the Restricted Area. The 640,000km^2 ‘no-take’ marine protected area (MPA), encompassing the Chagos Archipelago, also prohibits all commercial fishing and extractive activities.

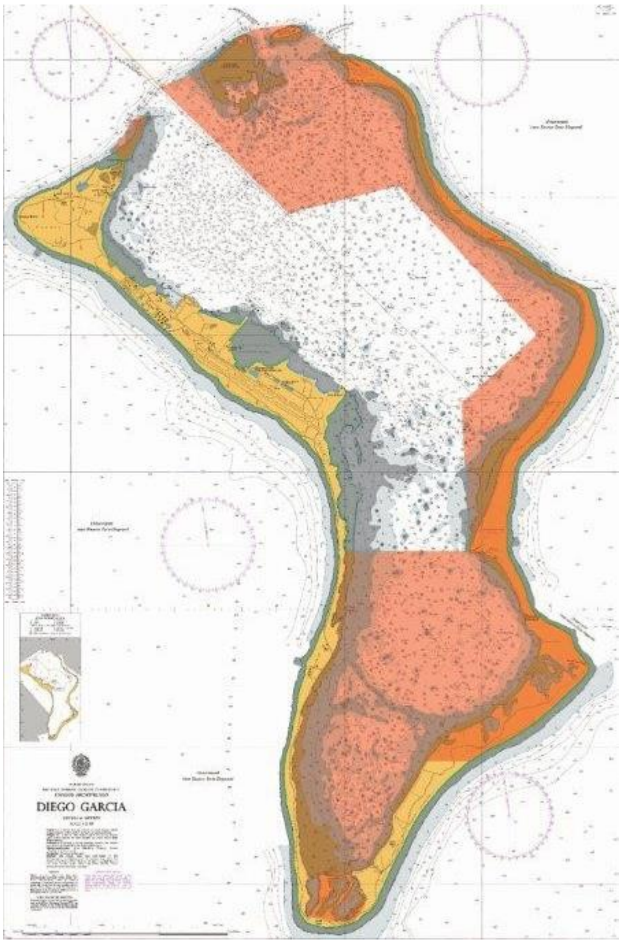

Figure 9.2. Map of the Restricted Area (red shaded) in Diego Garcia, Chagos Archipelago. Source: https://www.biot.gov.io/environment/terrestrial-protected-areas/

Green and hawksbill foraging and nesting habitats in the Chagos Archipelago are well-protected. Nonetheless, further research can improve our understanding of these species and management actions can aid population resilience. This thesis aimed to address some of the research gaps to further understand and protect these species. One key concern is the rat population on many islands in the Chagos Archipelago. In chapter five, rats were identified as a predator of green turtle eggs. If the rat population is left unmanaged, it may decrease hawksbill and green turtle nesting productivity. Rat eradication on the islands of the Chagos Archipelago is of research priority (Hays et al. 2020) and has been successful on several smaller outer islands of the Chagos Archipelago, including Île Vache Marine and Île Jacobin in 2014 (Benkwitt et al. 2021). However, rat eradication may be challenging on the inhabited island of Diego

Garcia and so improvements to monitor control measures and biosecurity are essential. The findings in this thesis (chapter five) were used as evidence for rat predation on sea turtle eggs and supported the application by the Environment Officers for funding to conduct trials to control and monitor rat populations on Diego Garcia using new rat trapping technology which was awarded for one year to be executed by 2025. As the study could only be conducted over the green turtle nesting season, the next steps are to identify hawksbill egg predation as well as quantify and monitor predation by rats on both green and hawksbill turtle hatchlings.

The upward trend in green and hawksbill turtle populations in the Chagos Archipelago is promising (Mortimer and Esteban et al. 2020), particularly as the archipelago is a nesting refuge for green turtles across the Western Indian Ocean. The upward trends are likely attributed to the long-term protection of both species in the archipelago, but further annual monitoring is required. Previously, although efforts were made to monitor the index nesting beach on Diego Garcia, the beach was monitored every two to four weeks with gaps due to reduced resources on the island. The surveys conducted during my PhD were more frequent over the green turtle peak nesting season in 2021 and 2022 and as survey support has increased on Diego Garcia with more Environment Officers, the continuity will hopefully remain to ensure accurate nesting population estimates. Many time-series datasets for sea turtle populations are too short-term to provide statistical significance in trends so longer time series data is essential (Mazaris et al. 2017). The use of camera traps to count tracks on the nesting beach (chapter six) will increase the temporal coverage, increasing the time series data to monitor and assess trends in the population. Future nesting number estimates will now also be improved as the data collected during my PhD includes the number of tracks resulting in egg-laying which was previously based on findings from the Seychelles (Mortimer et al. 2020).

Climate change related increasing temperatures and sea level rise have been highlighted as the greatest threats to sea turtle reproductive output by scientists and managers (e.g., green turtles in the northern Great Barrier Reef; Fuentes and Cinner 2010). Expanding findings from Diego Garcia (Esteban et al. 2016), across the Chagos Archipelago, the sand at nest depths is relatively cool (chapter four), compared to many sites globally where production of hatchlings has been female skewed (Hays et al. 2014). The cool sand temperatures (chapter four) are likely down to a combination of heavy rainfall and shading from vegetation of which we know green turtles predominantly nest under (chapter three). Hatching success, which had not previously been studied in the Chagos Archipelago and monitoring long-term sand temperatures was a priority for my PhD research and was addressed in chapters four and five. With the baseline dataset of green turtle nest site selection and hatching success along with the long-term temperature data helps us understand the potential effects of climate change on the population in the Chagos Archipelago and if necessary, help identify conservation mitigation measures that could be implemented. The findings from this thesis also support the efforts proposed to rewild islands in the Chagos Archipelago by removing rats and restoring more natural ecosystems.

Estimating the immature foraging population and their regional importance was also of high research priority. Chapter six of this thesis addressed this gap in knowledge to estimate the immature foraging population and found that the immature hawksbill population was the highest density recorded across comparable developmental sites in the world. With this baseline estimate, we can continue to monitor trends at this developmental site to inform conservation and management plans.

Key learning points

I gained knowledge and skills exploring the methods used to understand sea turtle ecology throughout my PhD. In hindsight, there are several ways that I could have approached different aspects, for example, using multiple methods to relocate nests, such as triangulation and flagging tape instead of the use of stakes (which were disturbed by other nesting turtles or washed away) in the first expedition which would have saved me hours of digging and increased the sample size. Also, conducting a smaller trial using surveillance cameras over nests for hatchling emergence and predation rates to test the settings and setup thoroughly in these conditions. I will take these lessons and incorporate what I have learnt throughout my PhD into my future research. Throughout the past four years, I have had the opportunity to form several collaborations which has strengthened my research in many ways, through feedback on fieldwork protocols, to analysis and publication writing. When producing manuscripts for my PhD chapters, I realised that producing manuscripts is more efficient and effective with collaboration to combine skills and learn from others within and outside of the field of sea turtle research.

Further Research

Further research ideas that have evolved during my PhD, has led to an opportunity to continue research as a postdoctoral researcher to further explore data collected during my PhD. Although the intentions for this thesis were to collect data on the ecology of sea turtles, particularly, nesting ecology, the data collected were solely from the nesting green turtle population. The next steps would be to collect data on the nesting ecology of hawksbill turtles, including nesting behaviour, track and nest counts, and predation. Our predation study was limited to observations and clutch counts and nest excavations to assess the level of predation. To further this research, efforts will be placed into setting cameras above nests to capture rates of predation. As our previous trials for this were unsuccessful, mostly down to issues around the set-up design (distance, position of available trees), we could trial traditional camera traps and surveillance camera settings for both green and hawksbill nests. The Environment Officers on island have recently been awarded funding for rat trapping on Diego Garcia and we are looking to collaborate to put funds towards cameras to assess predation rates as a baseline to compare future predation once rat trapping commences. Being able to assess predation using cameras will increase our understanding of when across the nesting season and where along the nesting beach predation may be more prevalent and assess the influence of nest site selection, temperature, and nest depth on levels of predation.

In addition to cameras for predation rates, the diet of ghost crab, coconut crabs, and rats could be explored to understand how much of their diet is dominated by sea turtles. A recent study by Avenant et al. (2023) combined methods of gut content analysis, DNA analysis of gut contents and stable isotope analysis. From DNA analysis of gut contents turtle was identified in >20% of crab guts. The same approach of combining dietary methods could be applied to understand the importance of sea turtle eggs and hatchlings to ghost crab, coconut crab, and invasive rats in the Chagos Archipelago.

As we provide the methodology in this thesis for the use of camera traps on nesting beaches, the next step will be to conduct estimates of nesting sea turtles from the camera traps and update population trends from Mortimer et al. 2020 with recent years of data. During foot patrol surveys, I also collected data for the number of tracks resulting in nests which has not been included in this thesis and so this data will be incorporated into the population estimate. I would also like to setup camera traps on outer islands with measures to minimise the risk of stolen cameras to conduct population estimates on the outer islands.

Our population abundance estimates of immature turtles at Turtle Cove has provided a baseline for comparison of future surveys. As the population estimates were high at Turtle Cove, we can start to investigate the links between hawksbill turtle density, food availability, body condition and predator abundance and establish the carrying capacity of Turtle Cove. The same methods used at Turtle Cove can also be applied to the oceanside reef flats for abundance estimates of immature and adult green and hawksbill turtles.

As GPS coordinates were collected for all nests, some from the same individuals (but a small sample size) I observed nest site fidelity (the tendency of females to return to the same specific site to nest). Through foot patrol surveys, satellite tracking and flipper tagging of nesting females the sample size could be increased to explore the distribution of nests along the beach and level of nest site fidelity at the index beach on Diego Garcia.

In conclusion, my future research interests are focussed on conservation ecology and ways in which we can incorporate sensing techniques (e.g., UAVs, camera traps) to facilitate our research at remote sites. These interests expand on previous findings from my PhD but the direction of this work during my postdoctoral research will be heavily based on research priorities and activities funded by the grant.

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APPENDICES

CHAPTER TWO: Supplementary Information

A global review of green turtle diet: sea surface temperature as a potential driver of omnivory levels

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Table S2.1. Reported diet composition of green turtles around the globe by Sub-region, location, habitat type and methods used. Sub-regions are based on the RMU map (Fig. 2.1, Wallace et al. 2010). Sub-region abbreviations refer to the following (moving from west to east): Pacific, North Central (Pacific NC); Pacific, East (Pacific E); Atlantic, Northwest (Atlantic NW); Atlantic, Southwest (Atlantic SW) Atlantic, East (Atlantic E); Mediterranean; Indian, Northwest (Indian NW); Indian, Southwest (Indian SW); Indian Northeast (Indian NE); Indian, Southeast (Indian SE); Pacific, Southwest (Pacific SW); Pacific, Northwest (Pacific NW); Pacific South Central (Pacific SC). Sample methods include Gut Content Analysis (GCA), Oesophageal Lavage (OEL), Mouth Contents (MC), Stable Isotope Analysis (SIA), Faecal Examination (FE) and Video). Food items are categorised and shown as percentage of diet taxa consumed. The category 'Other' is not always defined in studies and, where defined, includes substrate (shell, stone), cyanobacteria, very digested material, unidentifiable material and natural debris (e.g., bird feathers, wood fragments, roots). The analytical method conducted to determine percent contribution of food items includes: % Dry weight (%DW), % Wet weight (%WW), % Volume (%V), stable isotope analysis for carbon (C) nitrogen (N) sulphur (S), unquantified observation (obs), and number of bites (# bites or # events), % Index of Relative Importance (%IRI). Habitat type is represented by (S=sand, HS=hard sand, Mu=mud, E=estuary, SG=seagrass, A=algae, Soft=soft bottom, Hard=hard bottom, M=mangrove, RR=rocky reef, CR=coral reefs, Af=artificial, NR=not recorded). Reference numbers relate to study sites shown in Fig. 2.1.

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Size Class $^+$ Carapace Length (cm) mean; range**	**% Seagrass**	**% Macroalgae**	**% Terrestrial plants (e.g., mangrove)**	**% Animal matter**	**% Anthropogenic debris**	**% Other**	**Reference**	**Ref no.**
Pacific NC	USA, Hawaii, 6 main islands	A, CR	OEL	%V	2003	155	range=35-75	0	100	0	<0.1	0	0	Arthur & Balazs 2008	1a
Pacific NC	USA, Hawaii, O'ahu, Kāne'ohe Bay	SG, A	OEL	%V	2003	26	range=35-75	10	90	0	<0.1	0	0	Arthur & Balazs 2008	1b
Pacific NC	USA, Hawaii, Oahu, Kawela Bay	CR, S, RR	OEL	%V	1985	12	x=53.1; range=40.8-67.7	0	100	0	0	0	*	Balazs et al. 1987	2a
Pacific NC	USA, Hawaii, Molokai, Palaau	CR, RR, Mu, M	OEL	%V	1985	21	x=50.4; range=38.8-71.3	6.7	93.5	0	*	0	*	Balazs et al. 1987	2b
Pacific NC	USA, Hawaii, Lanai & Maunalua	CR, S	OEL	%V	1985	7	x=51; range=38.9-72.5	0	92.4	0	7.1	0	0	Balazs et al. 1987	2c
Pacific NC	USA, Hawaii, Maui, Kahului Bay	Af	OEL	%V	1985	7	x=76.8; range=44.8-90.2	0	100	0	*	*	*	Balazs et al. 1987	2d
Pacific E	USA, California, San Diego Bay	SG	SIA (skin)	C, N	2003-2008	86	x=89.9; range=49-115; n=74	~30	~15	NI	~55	NI	NI	Lemons et al. 2011	3
Pacific E	México, Baja California, Bahia de los Angeles	NR	GCA	%V	1995-1999	7	x=72cm	0	80	0	20	0	*	Seminoff et al. 2002	4a

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Size Class $^{+}$ Carapace Length (cm) mean; range**	**% Seagrass**	**% Macroalgae**	**% Terrestrial plants (e.g., mangrove)**	**% Animal matter**	**% Anthropogenic debris**	**% Other**	**Reference**	**Ref no.**
Pacific E	Mexico, Baja California, Bahia de los Angeles	NR	OEL	%V	1995-1999	101	x=75.8; range=50.4-96.6	0	97	0	3	0	0	Seminoff et al. 2002	4b
Pacific E	Mexico, Baja California, Bahía de los Angeles	NR	Video	# of events	1997-2002	34	x=79.6; range= 64.1-96.7	0	43	0	32	0	25	Seminoff et al. 2006	5
Pacific E	Mexico, Baja California, Laguna Ojo de Liebre	A, SG	OEL	%V	2008-2009	21	range=40-79.9	10.3	21.5	0	68.8	0	0	Rodríguez Barón 2010	6a
Pacific E	Mexico, Baja California, Punta Abreojos	A, SG, M	OEL	%V	2008-2009	15	range=40-79.9	35.6	44.6	0	0	0	12.8	Rodríguez Barón 2010	6b
Pacific E	Mexico, Baja California, Bahia Magdalena lagoon	A, SG, M	OEL	%V	2008-2009	23	range=40-59.9	5.2	90.6	1.9	0.6	0	0.1	Rodríguez Barón 2010	6c
Pacific E	México, Baja California, San Ignacio lagoon	NR	OEL	%V	2011-2016	55	x=68.3; range=47.0-79.0	0	91.3	0	4.7	0	3.8	Vejar Rubio 2016	7
Pacific E	Mexico, Baja California,	M, A	OEL	%V	2002	15	x=59.9; range=48.0-75.6	0	98.5	<1	<1	0	0	López-Mendilaharsu et al. 2008	8

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class $^+$ Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
	Estero Banderitas														
Pacific E	Mexico, Baja California, Bahia Magdalena lagoon	E, M, SG, Soft, RR, A	GCA	%V	2000-2002	12	x=55.5; range=47.7-76.9; n=11	10.1	74.7	3.2	9.9	0	2.1	López-Mendilaharsu et al. 2005	9a
Pacific E	Mexico, Baja California, Bahia Magdalena coastal	RR, SG, A	GCA	%V	2000-2002	12	x=67.7; range=49-87; n=11	63.4	36.1	0	0	0	0	López-Mendilaharsu et al. 2005	9b
Pacific E	Colombia, Cauca, Gorgona Park	E, CR, Soft, S	OEL	%DW	2003-2004	84	x=58.4; range=37.0-72.9; n=86	0	3.7	14.6	72.6	0	9.1	Amorocho & Reina 2007	10
Pacific E	Colombia, Cauca, Gorgona Park	CR, A, M, S	OEL	%V	2012	Black: 30 Yellow: 47	Black: x=63.9; range=52.3-73.2 Yellow: x=54.3; range=40.9-68.9	0	12.6	37.8	20.3	13.1	0	Sampson et al. 2018	11
Pacific E	Ecuador, Galapagos	RR, A, M	OEL	%V	2006-2007	65	range=46-95	0	82.3	5.0	8.8	0	3.9	Carrión-Cortez et al. 2010	12

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Size Class $^+$ Carapace Length (cm) mean; range**	**% Seagrass**	**% Macroalgae**	**% Terrestrial plants (e.g., mangrove)**	**% Animal matter**	**% Anthropogenic debris**	**% Other**	**Reference**	**Ref no.**
Pacific E	Peru, Sechura Bay	A, SG	GCA	%WW	2013-2014	27	x=53.7; range=40.5–67.0	0	23	0	69	8	0.1	Jiménez et al. 2017	13
Pacific E	Peru, San Andrés	NR	GCA	NR	1999-2000	13	range=51-85	3.6	44.6	0	37.3	14.5	0	de Paz et al. 2004	14
Pacific E	Peru, San Andrés	NR	GCA	%WW	1987	192	x=67.5; range=45-100; n=998	0	13.5	0	72.2	10.9	3.4	Quiñones et al. 2010	15
Pacific E	Peru, Bahia Paracas, La Aguada	S, Mu, A	OEL	%WW	2011	22	x=59.7; range=46.3-76.5	0	17.6	0	82.4	*	0	Paredes 2015	16
Atlantic NW	Bermuda, Bermuda Platform	CR, SG, M	SIA (skin)	C, N	2012-2013	157	x=38.4; range=25.1-68.9	55	22	NI	24	NI	NI	Burgett et al. 2018	17
Atlantic NW	Florida, Mosquito Lagoon	SG	OEL	%WW	1978	6	unk	88.6	7.6	0	0	0	3.4	Mendonca 1983	18
Atlantic NW	USA, Florida, Trident Submarine Basin	Af, A	OEL	%V	2008-2010	94	x=29.4; range=24.3-44.5	2.8	71.8	0	11.7	0.7	13.4	Holloway-Adkins & Hanisak 2017	19a
Atlantic NW	USA, Florida, Trident Submarine Basin	Af, A	OEL	%V	1999-2002	108	unk	10.2	87.1	0	0.6	0	6.8	Holloway-Adkins & Hanisak 2017	19b
Atlantic NW	USA, Florida, Trident	Af, A	OEL	%V	1993-1996	69	x=31.7; range= 20.0-52.0	6.5	82.1	0	2.8	2	6.5	Holloway-Adkins & Hanisak 2017	19c

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class ⁺ Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
	Submarine Basin														
Atlantic NW	USA, Florida, Indian River County	RR, A	OEL	%V	2003	40	x=39.5; range=27-56	0.1	96.1	0	1.3	0	2.4	Gilbert 2005	20
Atlantic NW	USA, Florida, Palm Beach County, Lake Worth Lagoon	E, SG	OEL	%V	2005-2013	31	x=40.4; range=24.6-62.3; n=100	94	2	0	0	0	4	Gorham et al. 2016	21
Atlantic NW	USA, Texas, middle coast	E, SG	GCA	%V	2007-2010	63	x=31.5; range=17.6-65.4	35.6	58.4	0.1	2.8	3.1	0	Howell et al. 2016	22a
Atlantic NW	USA, Texas, lower coast	SG, E	GCA	%V	2007-2010	51	x=37.9; range=15.5-69.6	77.1	20.9	0.1	1.7	0.2	0	Howell et al. 2016	22b
Atlantic NW	USA, Texas, South Padre Islands	SG, Mu, A, HS	OEL	%DW	1991-1993	76 samples from 47 individuals	x=38.9; range=20-60	34.2	61.3	0	*	0.2	4.27	Coyne 1994	23
Atlantic NW	Bahamas, Eleuthera, Starved Creek	A, SG	OEL	%DW	2015	8	x=43.5; range=34.2-59.2	~94	*	0	*	0	*	Gary 2017	24

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Size Class $^+$ Carapace Length (cm) mean; range**	**% Seagrass**	**% Macroalgae**	**% Terrestrial plants (e.g., mangrove)**	**% Animal matter**	**% Anthropogenic debris**	**% Other**	**Reference**	**Ref no.**
Atlantic NW	USA, Key West National Wildlife Refuge & adjacent waters	SG, Hard, S, Mu, CR	OEL	%V	2003-2012	62	x=49.4; range=31.6-100	80.7	11.1	0	5.5	0	1.9	Herren et al. 2018	25
Atlantic NW	Florida, Dry Tortugas National Park	SG	SIA (flipper)	C, N	2008-2015	61	x=35.7; range=22.3-51.5	45	31	NI	24	NI	NI	Roche 2016	26a
Atlantic NW	Florida, Dry Tortugas National Park	SG	SIA (flipper)	C, N	2008-2015	98	x=93.7; range=65.3-111.7	86	1	NI	13	NI	NI	Roche 2016	26b
Atlantic NW	Turks & Caicos Islands	SG, CR	GCA	%WW	2008-2010	92	x=52.8; range= 28.8-88.8; n=91	91.0	1.0	0	7.0	*	0	Stringell et al. 2016	27
Atlantic NW	US Virgin Islands, Teague Bay	SG, A, S, CR	FE	obs	1981	1	>36	99	*	0	*	0	0	Ogden et al. 1983	28
Atlantic NW	Nicaragua, Caribbean (N), Miskito & Little Sandy Bay Cays	SG, CR	GCA	%DW	1975-1976	174	Subadult – Adult	94.2	3.1	0	1.1	0	1.5	Mortimer 1981	29a
Atlantic NW	Nicaragua, Caribbean (S), Mudset	Soft, Mu,	GCA	%DW	1975-1976	64	Subadult – Adult	72.6	20.1	0	1.7	0	5.6	Mortimer 1981	29b

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class + Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
	& Set Net Cays														
Atlantic NW	Colombia, La Guajira peninsula, Puerto Santa Cruz	A, SG	GCA	%V	2016	5	x=43; range=27-87	25	71.8	0	3.2	0	0	Vasquez Carrillo 2017	30
Atlantic SW	Brazil, Pernambuco, Fernando de Noronha, PE	CR	OEL	%WW	2010-2013	19	x=50.5	7.2	86.6	0	<0.1	0	0	Santos et al. 2015	31a
Atlantic SW	Brazil, Bahia, Abrolhos	CR	OEL	%WW	2010-2013	24	x=52.3	53.2	44	0	0.4	0	0	Santos et al. 2015	31b
Atlantic SW	Brazil, Rio de Janeiro State, (Búzios, Cabo Frio & Arraial do Cabo)	A	SIA (muscular tissue)	C, N	2009-2010	45	x=34.9; range=27.3-48	NI	~95	NI	~5	NI	NI	di Beneditto et al. 2017	32
Atlantic SW	Brazil, State of Sao Paulo, Ubatuba	RR, A	GCA	%DW	1979-1980	4	range=33.1-45.2	0	100	0	0	0	0	Sazima & Sazima 1983	33
Atlantic SW	Brazil, São Paulo, Baía de Santos	NR	GCA	%IRI	2004-2006	8	Unk	34.8	2.1	21.6	31.2	7.4	3.1	Carvalho et al. 2008	34
Atlantic SW	Brazil, São Paulo, Cananéia	E	OEL	%V	2009	53 samples from 50	x=36.9; range=31-50	2.4	20.1	35.1	7.8	0	34.4	Nagaoka et al. 2012	35

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Size Class $^{+}$ Carapace Length (cm) mean; range**	**% Seagrass**	**% Macroalgae**	**% Terrestrial plants (e.g., mangrove)**	**% Animal matter**	**% Anthropogenic debris**	**% Other**	**Reference**	**Ref no.**
	Estuarine - Lagoon,					individuals									
Atlantic SW	Brazil, Arvoredo Marine Reserve	RR, A	OEL	%DW	2005-2008	30	>30.5	0	88.4	0	11.6	0	0	Reisser et al. 2013	36
Atlantic SW	Uruguay, Cerro Verde	RR, S	OEL	%V	2005	23	x=41; range=32.6-58.4	0	95	0	2.2	0	0	Darré Castell et al. 2005	37
Atlantic SW	Argentina, Samborombón Bay	E	GCA	%WW	2008-2011	62	x=38.5; range=31.3 – 52.2; n=54	0	4.5	9.6	59	0	26.9	González Carman et al. 2014	38
Atlantic E	Africa, Gulf of Guinea, São Tomé Island, Ilhéu das Cabras, Foraging Ground North	SG, A	SIA (skin)	C, N	2015	5	x=73.8; range=64.0-83.0	~25	~55	NI	~20	NI	NI	Hancock et al. 2018	39a
Atlantic E	Africa, Gulf of Guinea, São Tomé Island, Foraging Ground South	RR, A	SIA (skin)	C, N	2015	8	x=73.0; range=53.0-87.0	0	~70	NI	~30	NI	NI	Hancock et al. 2018	39b

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class $^{+}$ Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
Mediterranean	Croatia	NR	GCA	%WW	2001	1	40	8.9	2.2	0	69.8	0	19.1	Lazar et al. 2010	40
Mediterranean	Greece, Lakonikos Bay	SG	GCA	obs	2000-2001	2	range=30.5-34.5	~100	0	0	0	0	0	Margaritoulis & Teneketzis 2003	41
Mediterranean	Turkey, Samandağ Beach	NR	GCA	%WW	2010	1 (F)	72.0	25.1	70.2	0	0.2	0.3	4.2	Özdilek et al. 2015	42
Mediterranean	Tunisia, Gulf of Gabes	S, Mu	GCA	%WW	2006	1	45.0	10.5	0	0	89.5	0	0	Karaa et al. 2012	43a
Mediterranean	Tunisia, Gulf of Gabes	S, Mu	GCA	%WW	2006-2011	6	x=90.4; range=65.5-110	85.6	0.1	0	0	1.9	12.4	Karaa et al. 2012	43b
Indian NW	United Arab Emirates, Ras al Khaimah	SG, A, S, Mu	GCA	%DW	1997	5	>89	99.0	<1	0	<1	0	<1	Hasbún et al. 2000	44
Indian NW	Oman, Masirah Channel	HS	GCA	obs	1977-1979	9	Adults	72	28	0	0	0	0	Ross 1985	45
Indian NW	Yemen P.D., Khor Umaira	SG	GCA	obs	1972	5	Adults (F)	100	0	0	0	0	0	Hirth et al. 1973	46
Indian NW	India, Gulf of Mannar and Palk Bay	CR	GCA	%W	1971-1976	10	x=50.2; range=40.4-64.5	62	28.9	0	9.3	0	0	Agastheesapillai & Thiagarajan 1979	47
Indian SW	Seychelles, Cosmoledo &	SG, CR	GCA	%DW	1982-1983	28 (26M, 2F)	x=102.3; range=93-111	95	2	0	2	*	*	Stokes et al. 2019	48

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class + Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
	Farquhar Atolls					Males & Non-breeding females									
Indian NE	Australia, Cocos-(Keeling) Islands	SG	OEL	%DW	1999-2012	10	x=64.7; range=33.5-115.6; n=984	65.1	27.8	0	6.1	0	0	Whiting et al. 2014	49
Indian SE	Australia, WA, Shark Bay, Eastern Gulf	SG, S	OEL	%WW	2006	3	>40	15.7	84.3	0	0	0	0	Burkholder et al. 2011	50a
Indian SE	Australia, WA, Shark Bay, Eastern Gulf	SG, S	SIA (skin)	C, N	2006-2009	65	range=40-120	0	~80	NI	~20	NI	NI	Burkholder et al. 2011	50b
Indian SE	Australia, WA, Shark Bay, Eastern Gulf	SG, S	Video	# bites	1999-2003	17 (12 usable videos)	unk	3	54	0	43	0	0	Burkholder et al. 2011	50c
Indian SE	Australia, WA, Shark Bay, Eastern Gulf	SG, S	Video	# bites	2011-2013	99 deployments on 98 individuals	x=96.4; range= 72.5-115.0	30	29.4	0	40.4	0	0.2	Thomson et al. 2018	51

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class $^+$ Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
Indian SE	Australia, Ashmore reef	CR, SG, S	OEL	%DW	NR	38	x=50.2; range=36.6-87.9; n=51	89	11	0	0	0	*	Whiting et al. 2007	52
Pacific SW	Australia, NT, Gulf of Carpentaria	NR	GCA	obs	1984	2	range=100.5-114.5	100	0	0	0	0	0	Limpus & Reed 1985	53
Pacific SW	Australia, Qld., Torres Strait	CR	GCA	%DW	1979	44	range= 37-127	9.1	89.2	0	0.9	0	0.8	Garnett et al. 1985	54
Pacific SW	Australia, Torres Strait, Orman Reefs	CR, SG	GCA	%V	1997-1998	26	Adults	55.3	44.5	0	0.1	0	0.1	Andre et al. 2005	55
Pacific SW	Australia, Qld., Green Island	CR, SM, SG, A	OEL	%V	2004	85 samples from 76 individuals	x=49.1; range= 38.9-64.8; n=108	83.8	15.6	0	0.65	0	0	Fuentes et al. 2006	56
Pacific SW	Australia, Qld., Repulse Bay	SG	OEL	%DW	1992-1993	12	range= 99.4-111; n=5	97	1.1	0.6	0.9	0	0.4	Whiting & Miller 1998	57
Pacific SW	Australia, Qld., Shoalwater Bay	SG, M, CR	MC	obs	1989	20	range=40-120	~50	~10	~40	0	0	0	Limpus & Limpus 2000	58
Pacific SW	Australia, Qld, Shoalwater Bay	SG, M, RR	OEL	%V	2002-2004	146	range= 39.9-115.6	85.5	9.4	1.4	1.7	0	1.5	Arthur et al. 2009	59a

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class $^{+}$ Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
Pacific SW	Australia, Qld., Shoalwater Bay	SG, M, RR	SIA	C, N	2001	1	107.0	97.5	1.4	0.6	NI	NI	NI	Arthur et al. 2009	59b
Pacific SW	Australia, Qld., Port Curtis - Wiggins	E, A, M	OEL	%WW	2013	12	x=48.2; range=42.7-60.0	9.2	87.6	0.4	2.4	0	0.4	Prior et al. 2016	60a
Pacific SW	Australia, Qld., Port Curtis-Pelican Banks	SG	OEL	%WW	2013	47	x=87.2; range=42.1-114.3	99.5	*	0	0.3	0	0.1	Prior et al. 2016	60b
Pacific SW	Australia, Qld., Heron Reef	A	OEL	%V	1988-1990	408	x=78.5; range=39.5-115.5	0.1	98	0	1.7	0	0.2	Forbes 1996	61
Pacific SW	Australia, Qld., Moreton Bay	E, SG, M, Soft, A	OEL	%V	1991	240	Juvenile to subadult	~38	~45	~2	~2	0	~13	Read & Limpus 2002	62
Pacific SW	Australia, Qld., Moreton Bay, Flathead Gutter	SG, S, A	OEL	%V	1995	20	>40.7	45.7	47.3	0	6.8	0	0.2	Brand-Gardner et al. 1999	63
Pacific NW	Japan, Sanriku Coast,	NR	FE	%WW	2012-2015	25	x=49.1; range= 38.0-90.9	14.5	31	0	9.6	38.5	6.5	Fukuoka et al. 2016	64a

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Size Class + Carapace Length (cm) mean; range	% Seagrass	% Macroalgae	% Terrestrial plants (e.g., mangrove)	% Animal matter	% Anthropogenic debris	% Other	Reference	Ref no.
	Ofunato and Miyako														
Pacific NW	Japan, Sanriku Coast, Ofunato and Miyako	NR	Video	# of events	2007-2015	6	x=55.2; range= 44.5-81.0	0	74	0	4	10	12	Fukuoka et al. 2016	64b
Pacific NW	Japan, Main Islands, Shikoku	A	SIA (scute)	C, N	2010-2011	32	x=57.2; range= 37.6-91.3	NI	~61	NI	~39	NI	NI	Shimada et al. 2014	65a
Pacific NW	Japan, Nansei Islands, Yaeyama	SG, A	SIA (scute)	C, N	2010-2011	42	x=54.9 range= 42.5-83.0	~38	~44	NI	~18	NI	NI	Shimada et al. 2014	65b
Pacific SC	Fiji, Yadua Island & Makogai Island	SG, A, CR, S	SIA (skin)	C, N	2015-2016	77	range=43.5-89.0 Yadua Island: x=56.0 Makogai Island:x=59.3	13	17	NI	70	NI	NI	Piovano et al. 2020	66
Pacific SC	Tokelau, Fakaofo	NR	GCA	obs	1981	1	Unk	0	100	0	0	0	0	Balazs 1983	67

+Straight and curved carapace lengths not differentiated

*Presence of diet item

‡Video studies were calculated by number of feeding events consuming diet item by total number of feeding events

NI SIA studies where diet items are not included in the putative prey / habitat samples collected for mixing model analyses

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Table S2.2 Reported diet composition of green turtles excluded from the review due to the following reasons: Anthropogenic debris ingestion (Anthropogenic debris ingestion analysis only), Diet % not specified, Captive / fed diet, Sampling at nesting sites, Size, Stranded dead / diseased, Location not specified (Foraging location not specified). Set out by 12 sub-regions, location, habitat type and methods used. Sub-regions are based on the RMU map (Fig. 2.1, Wallace et al. 2010). Sub-region abbreviations refer to the following (moving from west to east): Pacific, North Central (Pacific NC); Pacific, East (Pacific E); Atlantic, Northwest (Atlantic NW); Atlantic, Southwest (Atlantic SW) Atlantic, East (Atlantic E); Mediterranean; Indian, Northwest (Indian NW); Indian, Southwest (Indian SW); Indian Northeast (Indian NE); Indian, Southeast (Indian SE); Pacific, Southwest (Pacific SW); Pacific, Northwest (Pacific NW). Sample methods include Gut Content Analysis (GCA), Oesophageal Lavage (OEL), Mouth Contents (MC), Stable Isotope Analysis (SIA), Faecal Examination (FE) Observation and Video). The analytical method conducted to determine percent contribution of food items includes: % Dry weight (%DW), % Wet weight (%WW), % Volume (%V), % Index of Relative Importance (%IRI) % Frequency of Occurrence (%FO), stable isotope analysis for carbon (C) nitrogen (N) sulphur (S), unquantified observation (obs), number of bites (# bites), Number (Nu), Dry mass (%DM), % Abundance (%A), Nutrient Analysis (NA). Habitat type is represented by (S=sand, HS=hard sand, Mu=mud, E=estuary, SG=seagrass, A=algae, Soft=soft bottom, Hard=hard bottom, M=mangrove, RR=rocky reef, CR=coral reefs, Af=artificial, Sar=Sargassum, NR=not recorded).

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^{+}$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Study in multiple regions Mediterranean Atlantic NW Pacific SW	Northern Cyprus USA, North Carolina Australia, Qld.	NR	GCA	Nu; %W	2011-2016 2016-2017 1993-2017	34 10 7	Anthropogenic debris ingestion	range=25-86 range=25-35 range=6-57	Duncan et al. 2019a	
Study in multiple regions Pacific NC Pacific SW	USA, Hawaiian, 7 sites Australia, Qld.,Shoalwater Bay & Moreton Bay	SG, A, CR	OEL	%V	2002-2004	331	Diet % not specified	NR	Arthur et al. 2008a	
Study in multiple regions Pacific NC Pacific SC	Central Pacific. Samoa-based & Hawaiian based Pelagic Fisheries	Oceanic	GCA	%DW	2012-2016	9	Anthropogenic debris ingestion	Pelagic phase	Jung et al. 2018	
Study in multiple regions Pacific NC Pacific SC	Central Pacific. Samoa-based & Hawaiian based Pelagic Fisheries	Oceanic	GCA	%DW	1993-2011	22	Location not specified	x=41.8	Wedemeyer-Strombel et al. 2015	
Study in multiple regions Pacific NC Pacific E	Hawaii, Peru & central North Pacific	NR	SIA	C, N	NR	4	Diet % not specified	NR	Arthur et al. 2014	Nutrient analysis
Pacific NC	Central North Pacific	Oceanic	GCA	%V	1990-1991; 1999-2004	10	Location not specified	x=48.1; range= 30.0-70.5	Parker et al. 2011	
Pacific NC	North Pacific. Hawaiian based longline fishery	Oceanic	GCA	Obs	1996-2000	2	Location not specified	x=61.8 range=55.6-67.9	Work & Balazs 2002	Diet % not specified
Pacific NC	Hawaii, O'ahu	A, SG	GCA	Obs	1978-2002	61	Diet % not specified	NR	Russell et al. 2003	

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class + Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Pacific NC	Hawaii, O'ahu, Maunalua Bay	NR	Obs	Obs	2009	1	Diet % not specified	NR	Vicente et al. 2019	
Pacific NC	USA, Hawaiian Islands	NR	OEL	%V	1975-2010	2471	Stranded dead / diseased	NR	Russell et al. 2011	Diet % not specified
Pacific NC	Hawaii, O'ahu	NR	GCA OEL	%WW; %FO	1978-1993	802	Diet % not specified	NR	Russell & Balazs 1994a	Non-natives
Pacific NC	Hawaii, Hawaii, O'ahu, Kāne'ohe Bay	NR	GCA OEL	%WW; %FO	1978-1992	755	Diet % not specified	NR	Russell & Balazs 1994b	
Pacific NC	USA, Hawaii, O'ahu, Kāne'ohe Bay	NR	GCA	%V	1977-2005	372	Stranded dead / diseased	NR	Russell & Balazs 2009	Diet % not specified
Pacific NC	USA, Hawaii, O'ahu, Kāne'ohe Bay	NR	GCA	%V	2005-2012	194	Stranded dead / diseased	NR	Russell & Balazs 2015	Diet % not specified
Pacific E	California, San Francisco	NR	SIA	C, N	1850s	1	Diet % not specified	NR	Conrad et al. 2018	
Pacific E	Mexico, Baja California, Laguna Ojo de Liebre (LOL), Laguna Guerrero Negro (GNO), Laguna San Ignacio (LSI)	NR	OEL	%FO	2016-2017	LOL:108 GNO:72 LSI:20	Diet % not specified	LOL: x=75.6 GNO: x=64.3 LSI: x=51.4	Reséndiz et al. 2019	
Pacific E	Mexico, Baja California, Laguna San Ignacio (LSI)	SG, A	GCA	Obs	NR	NR	Diet % not specified	NR	Riosmena-Rodriguez 2009	
Pacific E	Mexico, Baja California, Playa San Lázaro	NR	SIA (Skin & bone)	C, N	2012	Captive: 5 Wild: 25	Stranded dead / diseased	Captive: range=46-53 Wild: x=56.8; range=42-71	Turner Tomaszewicz et al. 2017	Captive / Fed diet
Pacific E	Mexico, Baja California, Playa San Lázaro, Gulf of Ulloa	NR	SIA (bone & skin)	C, N	2009-2012	62	Stranded dead / diseased	x=59.6; range=42-95	Turner Tomaszewicz et al. 2018	Diet % not specified

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^+$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Pacific E	Mexico, Baja California, Bahia Magdalena	S, SG, RR, A	GCA	%V	2002-2003	5	Diet % not specified	range=47-77	Talavera-Saenz et al. 2007	
Pacific E	Mexico, Baja California, Bahia Magdalena	A, SG	SIA (skin, blood)	C, N	2005-2007	29	Diet % not specified	x=60.9; Range=44.5-81.4	Santos Baca 2008	
Pacific E	Mexico, Baja California, Magdalena Bay	S, RR, SG, A, M	GCA	%V	2002-2003	8	Stranded dead / diseased	range=47-77	Riosmena-Rodriguez 2011	
Pacific E	Mexico, Gulf of California, Los Cabos, Cabo Pulmo National Park	CR, S	Obs	N/A	2018	1	Diet % not specified	42	Ramos et al. 2019	
Pacific E	Mexico, Oaxaca, Chacahua Lagoon	A	OEL	Obs; %FO	2009-2010	16	Diet % not specified	x=85.6; range=80.0-93.8	Karam-Martinez et al. 2017	
Pacific E	Mexico, Baja California, Laguna San Ignacio (LSI), Bahia Magdalena (BM), Punta Abreojos (PA)	SG, M, A, E	GCA OEL	NR	GCA: 2008 OEL:2009	GCA: several OEL: 9	Stranded dead / diseased	NR	Lopez-Calderon et al. 2010	
Pacific E	Colombia, Cauca, Gorgona Park	NR	OEL	%V	NR	Subadults:39 Adults:4	Diet % not specified	Subadults: x=59.7 Adults: x=73.4	Sánchez & Quiroga 2005	
Pacific E	Colombia, Gorgona National Park	S, CR	FE	%DW	2005	9	Captive / Fed diet	x=58.2; range=52.2-62.2	Amorocho & Reina 2008	
Pacific E	Peru, Peruvian Coast	Mainly oceanic	SIA (skin)	C, N	2003-2009	68	Location not specified	x=53.7; range=27-71.2	Kelez 2011	
Pacific E	Peru, Sechura Bay	NR	GCA	%F; %W	2003-2004	44	Diet % not specified	x=63.6; range=47.5-88	Santillán 2008	
Pacific E	Peru, San Andrés & Chimbote	NR	GCA	Obs	1999-2000	3	Diet % not specified	x=72; range=56-83.2	Sara et al. 2005	

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^{+}$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Atlantic NW	New York, Long Island	NR	FE; GCA	%FO; Obs	NR	25	Diet % not specified	range=25-40	Burke et al. 1991	
Atlantic NW	6 sites across Greater Caribbean	SG	SIA (skin)	C, N	2007-2011	376	Diet % not specified	range=30.8-122.1	Vander Zanden et al. 2013b	
Atlantic NW	Florida	Sar	OEL; FE	%DW	2006-2011	18	Size	ALL 44: x = 20.6	Witherington et al. 2012	
Atlantic NW	Florida, St. Joseph Bay	NR	GCA	%FO	2000-2001	44	Diet % not specified	ALL 387: x=36.6; range=25.0-75.3	Foley et al. 2007	
Atlantic NW	Florida, St. Joseph Bay	SG, A	GCA SIA (skin)	%V; %DW; %FO; %IRI C, N	2008 & 2011	2008: 12 2011: 31	Stranded dead / diseased	2008: x=30.4; range=23.6-35.9 2011: x=35.9; range=22.5-72.7	Williams et al. 2014	
Atlantic NW	Florida, Mosquito Lagoon, South Bay, Jennings Cove, Reef site	RR, E, S, SG	OEL GCA	%V; %FO	OEL: 1995-2001 GCA: 1989	Mosquito Lagoon: 59 South Bay: 61 Jennings Cove: 57 Reef site: 59	Stranded dead / diseased	Mosquito Lagoon:x=51.3; range=28.1-72.7 South Bay:x=45.3; range=28.1-72.7 Jennings Cove:x=52.8; range=32.7-72.1 Reef site:x=43.8; range=27.0-61.9	Holloway Adkins 2001	
Atlantic NW	Florida, Palm Beach County	RR, Hard, A	OEL	%FO	2003	6	Diet % not specified	x=36.7; range=27.9-48.1	Makowski et al. 2006	
Atlantic NW	Texas coast, Port Isabel & Port Aransas	SG, A	SIA (scute)	C, N	2007-2009	44	Diet % not specified	range=24.9-61.5	Gorga 2011	
Atlantic NW	Bahamas, Bimini	SG, A,	SIA (skin)	C, N	2016	58	Stranded dead / diseased	range=28.6-69.9	Gillis et al. 2018	
Atlantic NW	Bahamas, Great Inagua, Union Creek	NR	FE	Obs	NR	72	Diet % not specified	NR	Bjorndal 1990	Nutrient analysis

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Reason for exclusion**	**Size Class $^+$ Carapace Length (cm) mean; range**	**Reference**	**Additional Reasons for exclusion**
Atlantic NW	Bahamas, Great Inagua	NR	SIA (scute)	C, N	NR	44	Diet % not specified	<36	Reich et al. 2007	
Atlantic NW	Bahamas, Great Inagua, Union Creek & Costa Rica, Tortuguero	NR	SIA (scute)	C, N	2009	43	Diet % not specified	Juveniles-adults	Vander Zanden et al. 2013a	
Atlantic NW	Costa Rica, Tortuguero	S, Mu, RR	GCA	%FO	1958 1976-1977	1958: 2 1976-1977: 9	Sampling at nesting site	Adults (F)	Meylan 1978	Diet % not specified
Atlantic NW	Cuba, Villa Clara	NR	GCA	%FO	2014-2015	4	Stranded dead / diseased	range=51-54	Russet Rodríguez et al. 2019	
Atlantic NW	British West Indies, Grand Cayman, Cayman Turtle Farm	NR	NR	NA	NR	115	Captive / Fed diet	Hatchlings	Roark et al. 2009	Nutrient Analysis
Atlantic NW	British West Indies, Grand Cayman, Cayman Turtle Farm	NR	FE	NA	1979	300	Captive / Fed diet	14-month-old; 44-month-old	Wood & Wood 1981	
Atlantic NW	British West Indies, Grand Cayman, Cayman Turtle Farm	NR	SIA (blood & skin)	C, N	2003	8	Captive / Fed diet	x=45.2; range=43.0-47.5	Seminoff et al. 2006	
Atlantic NW	British West Indies, Grand Cayman	NR	SIA (skin)	C, N	2010	Adult F: 30 Juveniles: 40	Captive / Fed diet	Adult F: range=92-110 Juveniles: range=64-92	Vander Zanden et al. 2012	
Atlantic NW	Costa Rica, Tortuguero	SG	SIA (bone)	C	2000	7	Diet % not specified	From 3 individuals: range=93.0-108.0	Biasatti 2004	
Atlantic SW	Brazil, Ceará, Almofala; Canoa-Quebrada	NR	GCA	%FO	1965-1967	94	Diet % not specified	range=31-120	Ferreira 1968	

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Reason for exclusion**	**Size Class $^+$ Carapace Length (cm) mean; range**	**Reference**	**Additional Reasons for exclusion**
Atlantic SW	Brazil, Ceará & Bahia	A, CR, E	SIA (muscle & scute)	C, N	2009-2012	41	Stranded dead / diseased	x=36.0 range=25.4-62.0	Bezerra et al. 2015	
Atlantic SW	Brazil, Paraíba state	NR	GCA	%FO	2009-2010	106	Anthropogenic debris ingestion	x=56.6; range=24.0-123.5	Poli et al. 2014	Stranded dead / diseased
Atlantic SW	Brazil, State of Bahia, Praia do Forte	CR, A	GCA	%FO	2010-2013	22	Diet % not specified	x=40.6; range=26.5-113	Jardim et al. 2016	
Atlantic SW	Brazil, Espírito Santo state	NR	GCA	NR	NR	74	Anthropogenic debris ingestion	x=36.9; range=30.0-44.5	Santos et al. 2016	Stranded dead / diseased
Atlantic SW	Brazil, Espírito Santo state	A	GCA	%FO; %V; %DW	NR	15	Stranded dead / diseased	x=44.0; range=35.1-60.0	Santos et al. 2011	
Atlantic SW	Brazil, Espírito Santo state & Fundão	S, RR, E	GCA	%WW	NR	43	Stranded dead / diseased	x=35.2; range=29.0-45.2	Machovsky-Capuska et al. 2020	
Atlantic SW	Brazil, Espirito Santo, Regência beach	E	GCA	%DW; Nu	2014-2015	17	Anthropogenic debris ingestion	x=36.3; range=32.4-40.0	Ferreira 2015	
Atlantic SW	Brazil, Trindade Island	RR, S, A, CR	SIA (skin)	C, N	2017	40	Diet % not specified	range=88-111	Rezende Barreto 2018	
Atlantic SW	Brazil, Rio de Janeiro	NR	GCA	%FO	2009-2010	37	Stranded dead / diseased	x=35.0; range=27.3-49.0	Awabdi & Siciliano 2013	Diet % not specified
Atlantic SW	Brazil, São Paulo, Ubatuba & Ilhabela	E	GCA	%FO	2013-2014	23	Diet % not specified	range=30-79	Romanini 2014	
Atlantic SW	Brazil, São Paulo, Ubatuba	NR	GCA	%FO	2008-2009	20	Anthropogenic debris ingestion	range=33-44	Silva Mendes et al. 2015	Stranded dead / diseased

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^+$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Atlantic SW	Brazil, São Paulo, Ubatuba & Florianópolis	NR	GCA SIA	%FO; %V; %IRI C, N	2016-2017	Ubatuba: 34 Florianópolis: 38	Stranded dead / diseased	Ubatuba: x=42.0; range=30.5-61.6 Florianópolis: x=31.6; range= 26.4-46.2	Souza 2019	
Atlantic SW	Brazil, Florianópolis, Mole Beach	NR	GCA	%DW; Nu	2010	1	Anthropogenic debris ingestion	39	Stahelin et al. 2012	Stranded dead / diseased
Atlantic SW	Brazil, São Paulo, Itapoá	RR, S, M, A, SG	GCA	%FO, %IRI; %DW	2012-2015	38	Stranded dead / diseased	x=41.4; range=27.2-70.7	Souza 2016	
Atlantic SW	Brazil, Paraná	E, SG, CR	GCA	%V; %WW	2008-2014	120	Stranded dead / diseased	x=40 range=30-62	Gama et al. 2016	
Atlantic SW	Brazil, Paranaguá Estuary	E, M, RR, S, SG, A	GCA	%V	2004-2007	80	Stranded dead / diseased	x=49.7; range=29-73	Guebert-Bartholo et al. 2011	
Atlantic SW	Brazil, Santa Catarina State	NR	GCA	Obs	2006-2009	27	Stranded dead / diseased	NR	Morais et al. 2012	Diet % not specified
Atlantic SW	Brazil, Santa Catarina State	RR, E	GCA	%WW	2006-2009	26	Stranded dead / diseased	x=35.8; range=23.5-50.0	Morais et al. 2014	
Atlantic SW	Brazil, Alagoas to Santa Catarina	RR, E	GCA	%DW;Nu	2009-2013	295	Anthropogenic debris ingestion	x=37.9; range=26.1-78.4	Andrades et al. 2019	Stranded dead / diseased
Atlantic SW	Brazil, Rio Grande do Sul	S, Mu, Hard, A	GCA	%FO; Nu	1997-1998	38	Stranded dead / diseased	x=37.7; range=28-50	Bugoni 2003	
Atlantic SW	Brazil, Rio Grande do Sul	NR	GCA	%V; %FO	1994-2006	64	Stranded dead / diseased	x=39.7; range=29.0-67.0	Nakashima 2008	
Atlantic SW	Brazil, Rio Grande do Sul	NR	GCA	%FO	NR	9	Stranded dead / diseased	x=37.7; range=32.5-43	Barros et al. 2007	Diet % not specified

Sub-region	**Location**	**Habitat Type**	**Method**	**Analysis**	**Year(s)**	**Sample Size**	**Reason for exclusion**	**Size Class $^+$ Carapace Length (cm) mean; range**	**Reference**	**Additional Reasons for exclusion**
Atlantic SW	Brazil, Rio Grande do Sul	NR	GCA	%FO; Nu; %DW	2011-2014	62	Anthropogenic debris ingestion	x=37.3; range=31.0-44.4	Colferai et al. 2017	Stranded dead / diseased
Atlantic SW	Brazil, Rio Grande do Sul	S, Mu, Hard, A	GCA	%FO; %DW	1997-1998	38	Anthropogenic debris ingestion	x=37.7; range=28-50	Bugoni et al. 2001	Stranded dead / diseased
Atlantic SW	Brazil, Rio Grande do Sul	NR	GCA	%DW	2006-2007	29	Anthropogenic debris ingestion	x=40.1; range=32.5-56	Silva Tourinho 2007	Stranded dead / diseased
Atlantic SW	Uruguayan coast	NR	GCA	%FO	2009-2013	54	Location not specified	x=40.0; range=29.8-62.0	Velez-Rubio et al. 2015	Stranded dead / diseased; Diet % not specified
Atlantic SW	Uruguayan coast	NR	GCA	%FO; %V; %DW	2005-2013	96	Anthropogenic debris ingestion	x=40.2; range=29.8-62.0	Velez-Rubio et al. 2018	Stranded dead / diseased
Atlantic SW	Uruguayan coast	E	OEL; GCA; SIA	%FO; %V; %IRI C, N	OEL: 2003-2005 GCA: 2009-2013 SIA: 2012-2013	OEL: 74 GCA: 52 SIA:126	Location not specified	OEL: range=32.6-58.4 GCA: range=29.8-62.0 SIA: range=27.8-66.8	Velez-Rubio et al. 2016	Stranded dead / diseased
Atlantic SW	Argentina-Uruguay, Río de la Plata	E	GCA	%WW; %FO	2008-2011	62	Anthropogenic debris ingestion	x=38.5; range=31.3-52.2	González Carman et al. 2014	
Atlantic E	Canary Islands	A, SG	SiA (scute)	C, N	2014	12	Captive / Fed diet	range=41.5-81.0	Monzon-Arguello et al. 2018	
Atlantic E	Mauritania, Banc d’Arguin	SG, A, Mu	SIA (scute)	S, N	2006	19	Diet % not specified	x=47.1; range=29-102	Cardona et al. 2009	

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class ⁺ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Mediterranean	Southern Greece, Cyprus & Israel	SG, A	SIA (scute)	C, N	2006-2008	22	Location not specified	range=29-83	Cardona et al. 2010	Stranded / diseased; Diet % not specified
Mediterranean	Cyprus	NR	GCA	%DW	2011-2013 2014-2016	2011-2013: 15 2014-2016: 19	Anthropogenic debris ingestion	x=36.9; range=25-86	Duncan et al. 2019b	
Mediterranean	Cyprus	NR	FE	NR	NR	12	Captive / Fed diet	1-year-old	Hadjichristophorou & Grove 1983	
Indian NW	United Arab Emirates, Sharjah, Kalba & Khorfakkan	NR	GCA	%FO; Nu; %DW	2016-2017	14	Anthropogenic debris ingestion	x=62.7; range=36.0-89.0	Yaghmour et al. 2018	Stranded dead / diseased
Indian NW	Oman, Ra's Al Hadd	NR	GCA	%FO; %DW; %IRI	2001	15	Stranded dead / diseased	range=43-111	Ferreira et al. 2006	
Indian SW	Seychelles, Aldabra	SG, A, CR	GCA	%FO	1967-1968	6 (Adult males (4) and subadult females (2))	Diet % not specified	x=94.1; range=84.5-101.5	Frazier 1971	
Indian SW	Comoros Archipelago, Mayotte Island, Bay of N'Gouja	SG, S, Mu	Obs	Obs	2004-2005	700	Diet % not specified	Small individuals: SCL < 80 (x=48.9; range=39-58.5; n=7) Large individuals: SCL > 80 (x=94.5; range=83-105)	Ballorain et al. 2010	
Indian SW	Reunion Island	NR	GCA	Obs	1998-2001	3	Diet % not specified	x=107.7may range=100-117	Ciccione 2001	
Indian NE	Thailand, Phang-Nga, Huyong Island	NR	FE	NR	NR	138	Captive / Fed diet	10-days-old to 3-month-old	Kanghae et al. 2017	

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^+$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Indian NE	Thailand, Phang-Nga, Huyong Island	NR	FE	NR	NR	NR	Captive / Fed diet	45-day-old	Kanghae et al. 2014	
Indian NE	Thailand, Phuket	NR	FE	NR	NR	3	Captive / Fed diet	4-month-old	Thongprajukaew et al. 2016	
Indian NE	Thailand, Phuket	NR	FE	NR	NR	NR	Captive / Fed diet	Five-days-old	Kanghae et al. 2014	
Indian SE	Australia, WA, Port Hedland, North Turtle Islands & Paradise Beach North	CR, A, SG	SIA (scute)	C, N	2009	2	Diet % not specified	Adult	Foster & Oates 2010	
Indian SE	Australia, WA, Shark Bay, Eastern Gulf	SG, S	Video	Obs	1999-2000	12	Diet % not specified	range=76-103	Heithaus et al. 2002	
Pacific SW	Australia, Qld., Raine Island (Internesting females on nesting beach)	NR	GCA	%DW	1997	11; 60% of 101 had empty guts	Sampling at nesting site	x=104; range: 92-118	Tucker & Read 2001	
Pacific SW	Australia, Qld., Howick Group of reefs, Cleveland Bay & Upstart Bay	SG, A, CR, M	OEL	Obs	2014-2017	NR (A subset of 3643)	Diet % not specified	Juvenile to Adult	Bell et al. 2019	
Pacific SW	Australia, Great Barrier Reef, Cairns	NR	GCA	Obs, Nu	NR	2	Anthropogenic debris ingestion	45.4 & 103	Caron et al. 2018	
Pacific SW	Australia, Qld., Shoalwater Bay	SG, M, RR	OEL	%V	2002	46	Duplicate dataset	Immature to adult range=~40-115	Arthur et al. 2006	
Pacific SW	Australia, Great Barrier Reef, Heron Island Reef & Wistari Reef	CR	Obs	Obs	NR	NR	Diet % not specified	range=38-120	Limpus 1979	

Sub-region	Location	Habitat Type	Method	Analysis	Year(s)	Sample Size	Reason for exclusion	Size Class $^{+}$ Carapace Length (cm) mean; range	Reference	Additional Reasons for exclusion
Pacific SW	Australia, Qld., Wreck Rock, Fraser Island & Gold Coast	NR	SIA (tissue)	C, N	NR	64	Stranded dead / diseased	Hatchling to Adult	Arthur et al. 2008b	Diet % not specified; Size
Pacific SW	Australia, Qld., Moreton Bay	SG	Video	Obs	2007	8	Diet % not specified	x=98.8; range=88.0-106.1	Arthur et al. 2007	
Pacific SW	Australia, Qld., Moreton Bay, Flathead Gutter	SG, S, A	OEL	%V	1994-1995	3	Duplicate dataset	x=52.7; range=50.3-55.2	Brand et al. 1999	
Pacific SW	Australia, Qld., North Stradbroke Island	NR	GCA	%FO; %A	2006-2013	88	Anthropogenic debris ingestion	NR	Schuyler et al. 2012 Schuyler et al. 2014	
Pacific SW	Australia, New South Wales & Qld.	NR	Obs	Obs	NR	Stranded: 31 From fish stomachs: 17	Size	Stranded: x=7.7; range=5.5-11.3 From fish stomachs: x=7.3; range=5.9-9.4	Boyle & Limpus 2008	
Pacific SW	New Zealand, North Island	A, SG, CR	GCA	%FO; %V	2006-2013	29	Stranded dead / diseased	x=53.6; range=37.3-94.6	Godoy 2016	
Pacific NW	Japan, Sanriku Coast	SG, A	SIA (blood)	C, N	2012-2015	40	Diet % not specified	x=48.3; range=36.8-90.9	Fukuoka et al. 2019	
Pacific NW	Japan, Ogasawara post-nesting, Philippine Sea	69% Neritic 31% Oceanic	SIA (egg yolks)	C, N	2003-2004	89 F	Sampling at nesting site	range:87.1-109.2	Hatase et al. 2006	
Pacific NW	Hong Kong	NR	GCA	Obs	2011-2013	8	Stranded dead / diseased	x=58; range=34-81	Ng et al. 2016	

+Straight and curved carapace lengths not differentiated

‡Video studies were calculated by number of feeding events consuming diet item by total number of feeding events.

NR Information not reported

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Figs. S1.1-S1.4 Comparison of green turtle diet composition across the globe. Expanded version of Fig. 2.1 showing details of regional seagrass distribution and the six categories of diet items. S2.1 Atlantic ocean (East); S2.2. Atlantic ocean and Mediterranean sea; S2.3. Indian ocean; S2.4. Pacific ocean (West). The proportion of contribution made by six categories of diet items recorded in 89 datasets at 75 sites are shown by segments of the pie charts. The term 'Other' is not always defined and includes substrate, very digested material and natural debris (e.g., feathers). Methods used to study diet are represented by coloured lines—i.e., gut content analysis (black line), oesophageal lavage (blue line), SIA (orange line), observation (purple line) and animal-borne camera (red line) studies. Green dots indicate known seagrass observation data points (Source: UNEP-WCMC and Short, 2018, see Appendix Fig. S2.1-S2.4 for fine scale maps). Numbers indicate source literature (see Appendix Table S2.1 for study site, analytical method, diet group and results).

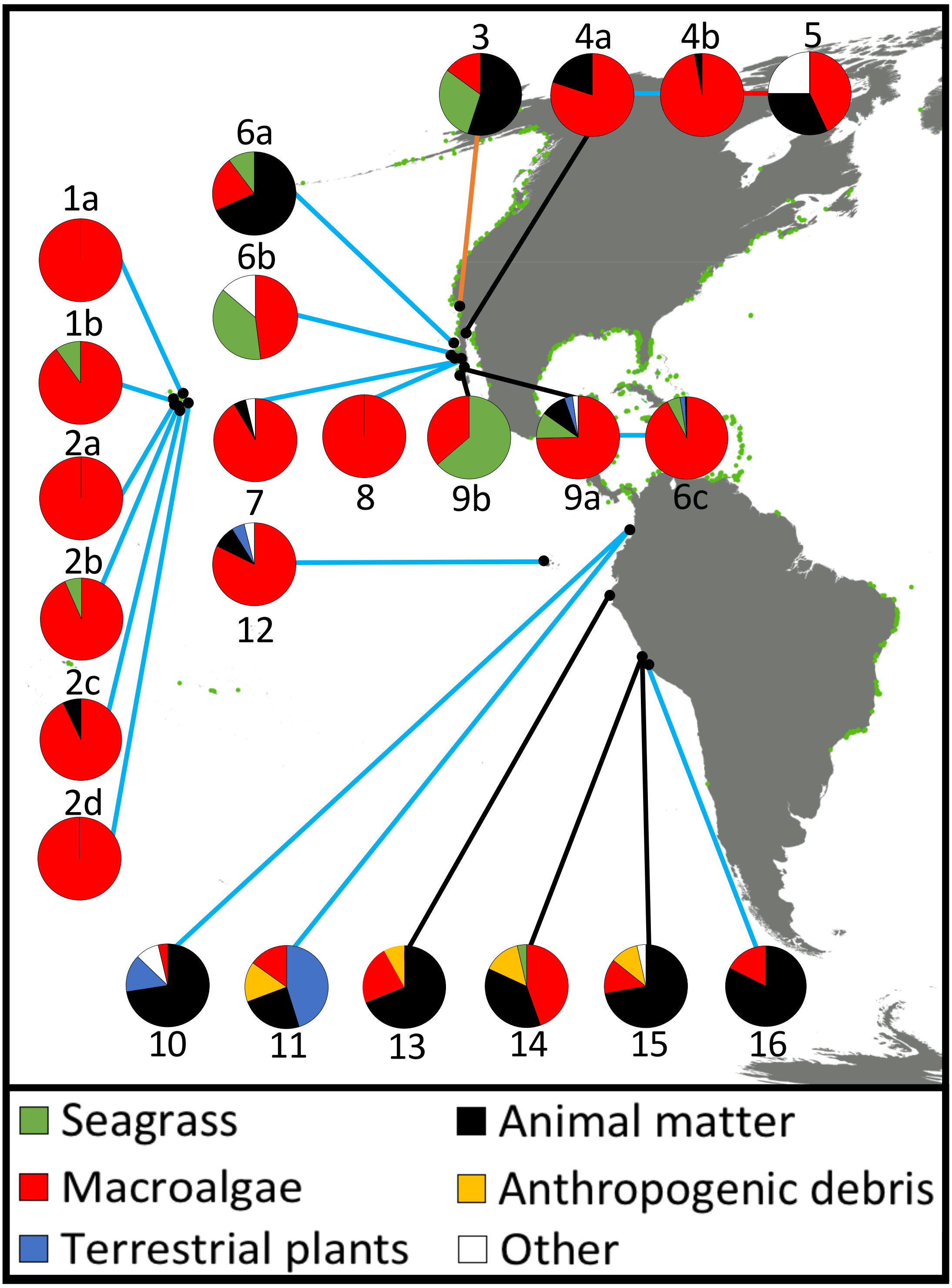

Figure S2.1. Comparison of green turtle diet composition across the globe: Atlantic Ocean (East)

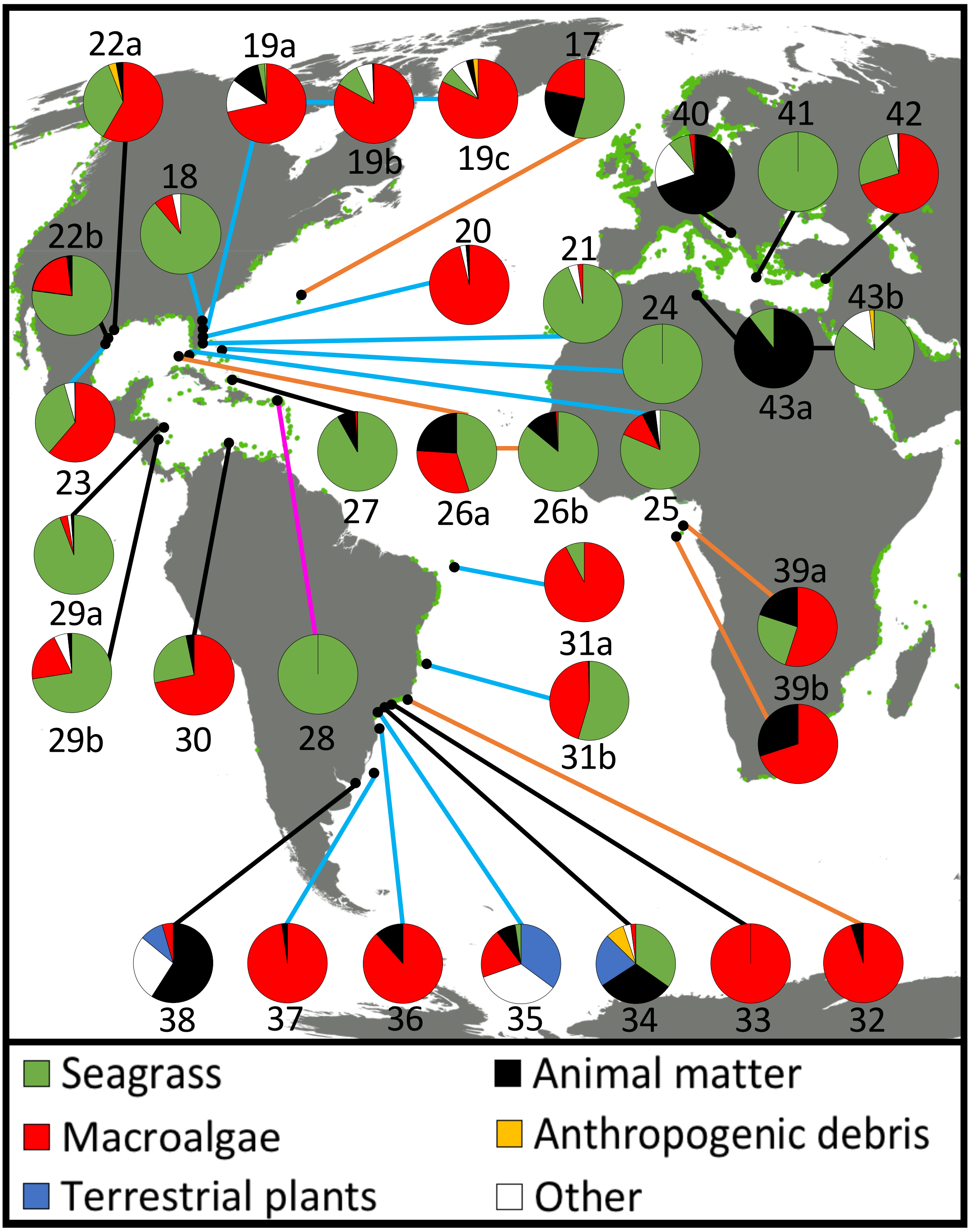

Figure S2.2. Comparison of green turtle diet composition across the globe: Atlantic Ocean and Mediterranean sea.

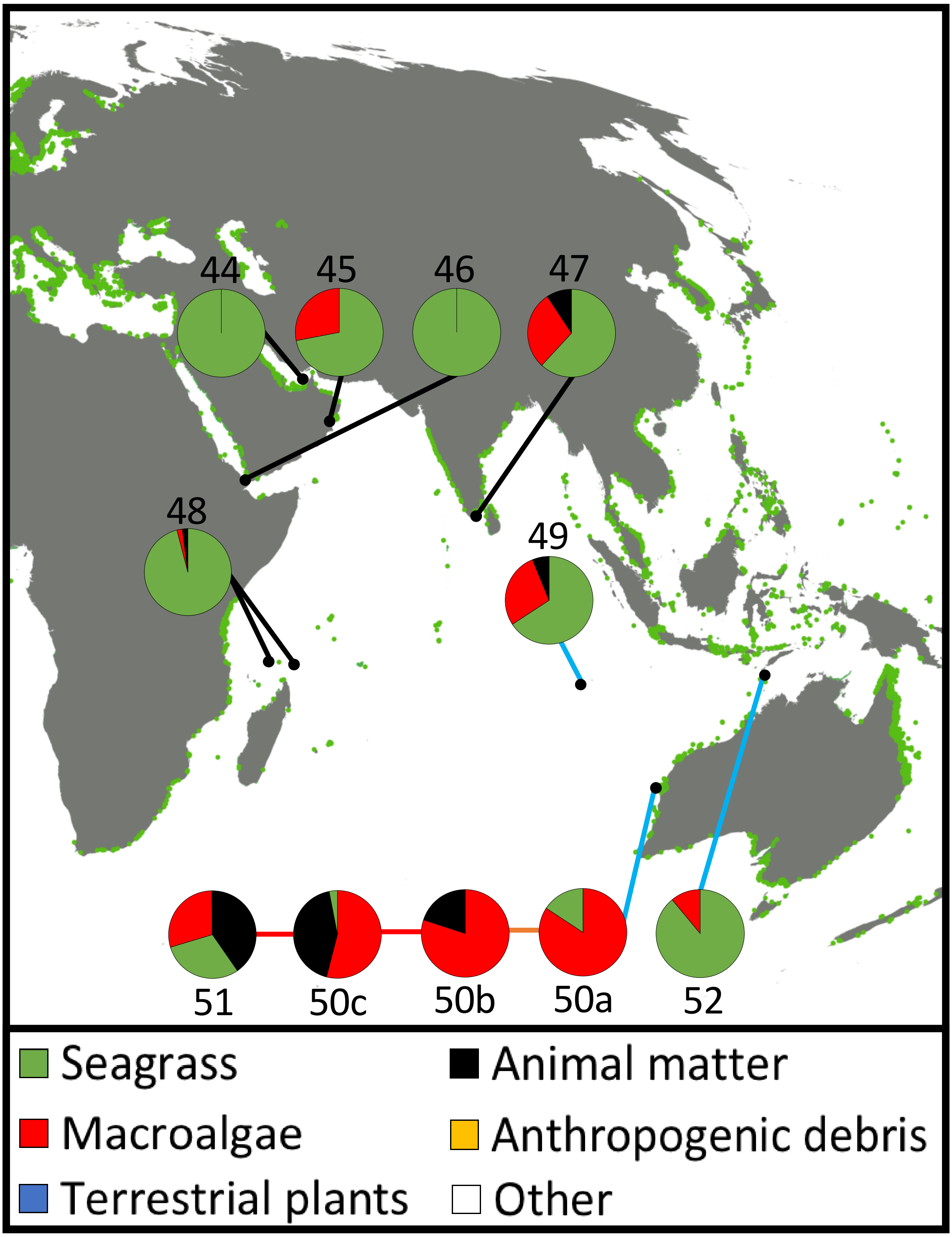

Figure S2.3. Comparison of green turtle diet composition across the globe: Indian Ocean.

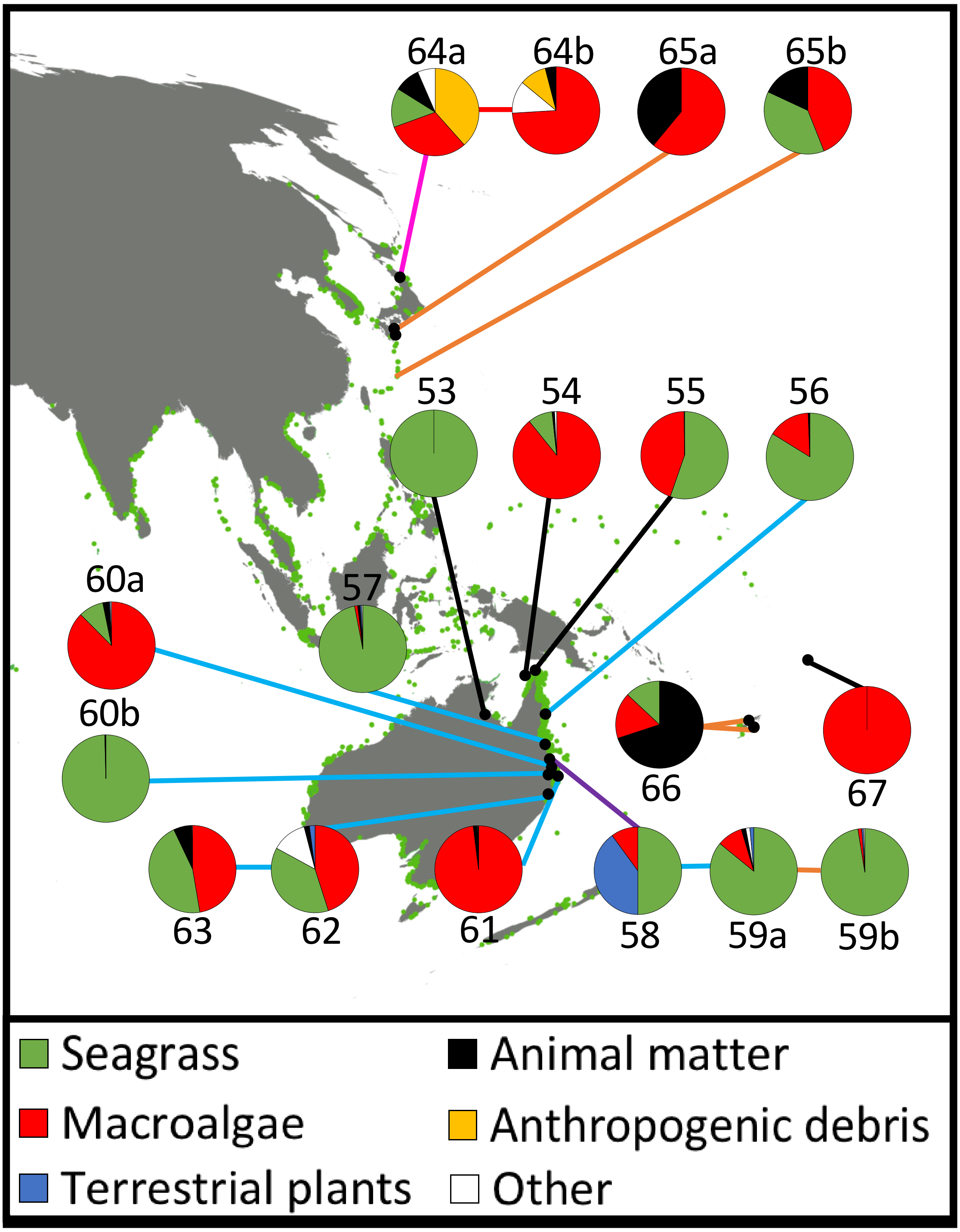

Figure S2.4. Comparison of green turtle diet composition across the globe: Pacific Ocean (West).

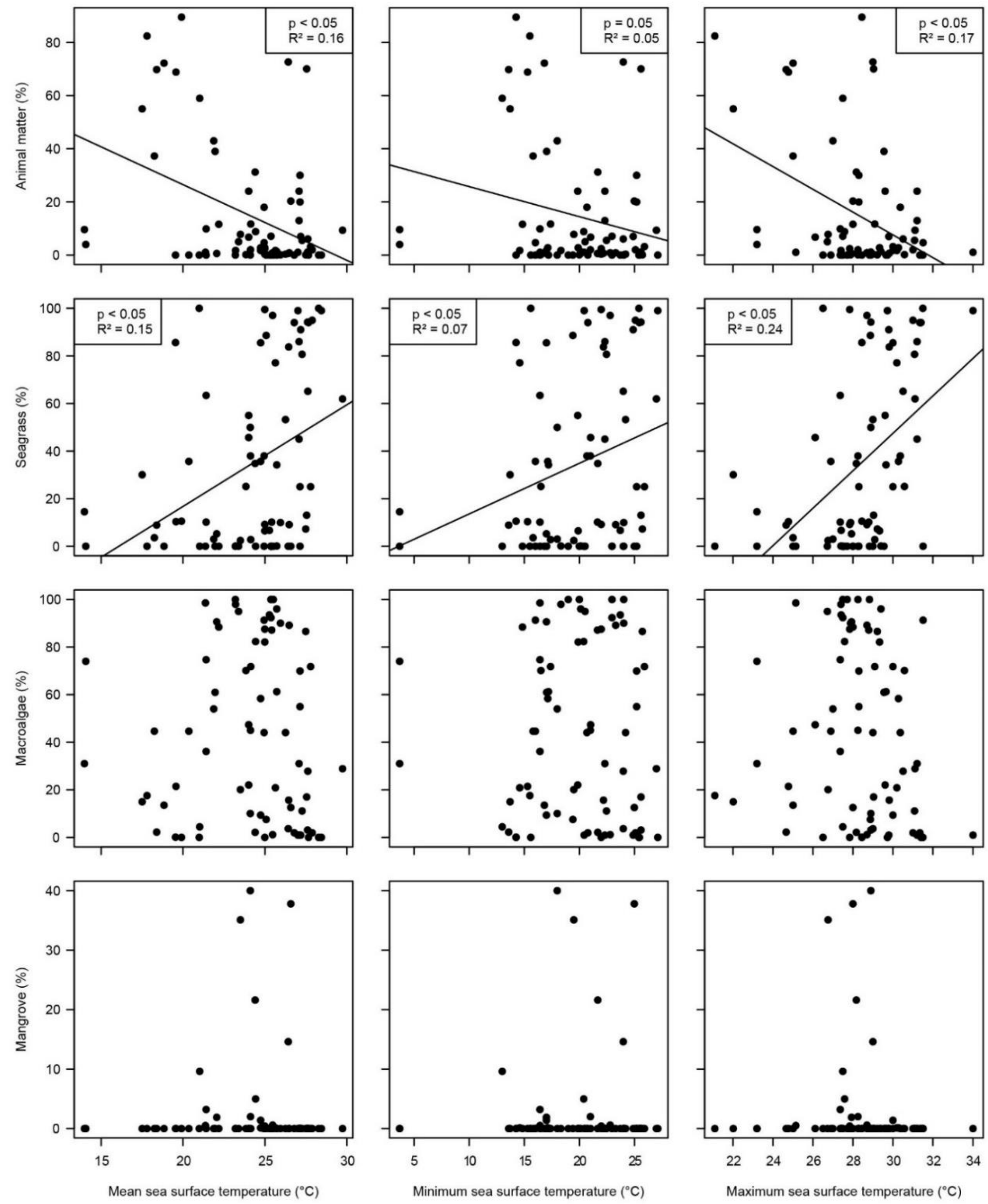

Figure S2.5. Sea surface temperature has a small but significant effect on animal matter and seagrass % composition in green turtle diet at foraging grounds (rows 1-2 respectively). There is no effect of temperature on macroalgae and mangrove composition in the diet (rows 3-4 respectively). Significant relationships are indicated by presence of a regression line, and R² and P value. A lower proportion of animal matter (and higher proportion of seagrass) is present in the diet of turtles at sites with higher sea surface temperatures. Sea surface temperature (from left to right: mean, minimum, maximum) is annual temperature recorded during the sampling year(s) of 82 datasets from 72 sites in the Atlantic, Indian and Pacific oceans and Mediterranean sea. SST (ICOADS) data source: NCAR 2015.

References to Supplementary Figure S2.5

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CHAPTER THREE: Supplementary Information

This work was published as:

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Table S3.1. Sea turtle nest distribution studies around the world, including the general study location, sea turtle species, and the beach zone where nests were predominantly found. Number corresponds to the number displayed in fig 3.5.

Number	General location (list of study sites)	Sea turtle species	Beach zone	References
1	Diego Garcia, Chagos Archipelago	Green (*Chelonia mydas*)	In vegetation	Current study
2	Redang and Penang Island, Malaysia	Green (*Chelonia mydas*)	In vegetation	Sarahaizad et al. 2012; Mohd Salleh et al. 2018; Mohd Salleh et al. 2021
3	Tambelan Archipelago, Indonesia	Green (*Chelonia mydas*)	In vegetation	Rumaida et al. 2021
4	Penghu Archipelago, Taiwan	Green (*Chelonia mydas*)	In vegetation	Wang and Cheng 1999; Chen et al. 2007
5	Veracruz and Quintana Roo, Mexico	Green (*Chelonia mydas*)	In vegetation	Zavaleta-Lizárraga and Morales-Mávil 2013; Santos et al. 2017
6	Cabuyal, Costa Rica	Green (*Chelonia mydas*)	In vegetation	Heredero Saura et al. 2022
7	Manabí, Ecuador	Green (*Chelonia mydas*)	In front of vegetation	Carpio Camargo et al. 2020
8	Wia-Wia Nature Reserve, Suriname	Green (*Chelonia mydas*)	In vegetation	Whitmore and Dutton 1985
9	Ascension Island	Green (*Chelonia mydas*)	Open beach above high water line	Hays et al. 1995
10	Bijagós Archipelago, Guinea-Bissau	Green (*Chelonia mydas*)	Open beach above high water line	Patrício et al. 2018
11	Akyatan Beach, Turkey	Green (*Chelonia mydas*)	In vegetation	Turkozan et al. 2011
11	Akyatan Beach; Dalaman-Sarigerme beach Turkey	Loggerhead (*Caretta caretta*)	In front of vegetation	Kaska et al. 2010; Turkozan et al. 2011
12	Yakushima Island, Japan	Loggerhead (*Caretta caretta*)	In front of vegetation	Hatase and Omuta 2018
13	Sunshine coast, Australia	Loggerhead (*Caretta caretta*)	In front of vegetation	Kelly et al. 2017
14	Sanibel and Captiva Islands; Boca Raton; Ten Thousand Islands; Boca Raton, Juno Beach,	Loggerhead (*Caretta caretta*)	In front of vegetation	Hays et al. 1995; Salmon et al. 1995; Garmestani

	Hutchinson Island, Archie Carr National Wildlife Refuge, and Canaveral National, Florida Seashore			and Percival 2000; Gravelle and Wyneken 2022
15	Bahia, Brazil	Loggerhead (*Caretta caretta*)	In front of vegetation	Serafini et al. 2009; Santos et al. 2016
16	Boa Vista Island, Cape Verde	Loggerhead (*Caretta caretta*)	Open beach above high water line	Martins et al. 2022a
17	Cephalonia Island and Zákynthos, Greece	Loggerhead (*Caretta caretta*)	In front of vegetation	Hays and Speakman 1993; Karavas et al. 2005
18	El Salvador and Estero Padre Ramos, Nicaragua	Hawksbill (*Eretmochelys imbricata*)	In vegetation	Liles et al. 2015
7	Manabí, Ecuador	Hawksbill (*Eretmochelys imbricata*)	In front of vegetation	Carpio Camargo et al. 2020
19	Trois Ilets and Folle Anse beaches, Guadeloupe	Hawksbill (*Eretmochelys imbricata*)	In vegetation	Kamel and Mrosovsky 2005
20	Barbados	Hawksbill (*Eretmochelys imbricata*)	In vegetation	Horrocks and Scott 1991
15	Bahia, Brazil	Hawksbill (*Eretmochelys imbricata*)	In vegetation	Serafini et al. 2009; Santos et al. 2016
21	Qatar; Shidvar Island, Iran; Nakhiloo, Ommolkaram and Nayband Bay in Bushehr Province, Persian Gulf	Hawksbill (*Eretmochelys imbricata*)	In front of vegetation	Ficetola 2007; Zare et al. 2012; Nasiri et al. 2022
22	Cousine Island, Seychelles	Hawksbill (*Eretmochelys imbricata*)	Open beach above high water line	Gane et al. 2020
23	Playa Gandoca; Tortuguero, Costa Rica	Leatherback (*Dermochelys coriacea*)	Open beach above high water line	Spanier 2010; Neeman et al. 2015
8	Wia-Wia Nature Reserve, Suriname	Leatherback (*Dermochelys coriacea*)	Open beach above high water line	Whitmore and Dutton 1985
24	Awala Yalimapo beach, French Guiana	Leatherback (*Dermochelys coriacea*)	In front of vegetation	Caut et al. 2006
25	Andaman Islands, India	Leatherback (*Dermochelys coriacea*)	In front of vegetation	Sivasunder and Devi Prasad 1996

26	Cabo Pulmo, Baja California peninsula, Mexico	Olive ridley (*Lepidochelys olivacea*)	Open beach above high water line	López-Castro et al. 2003
27	El Naranjo Beach, Nayarit, Mexico	Olive ridley (*Lepidochelys olivacea*)	Open beach above high water line	Hart et al. 2014
28	Piro and Pejeperro, Osa Peninsula, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	In front of vegetation	Ávila-Aguilar 2015
29	Fog Bay, Northern Territory, Australia	Olive ridley (*Lepidochelys olivacea*)	Open beach above high water line	Blamires and Guinea 1998
30	Fog Bay; Bare Island, Northern Territory; Mundabullangana, Western Australia, Australia	Flatback (*Natator depressus*)	Open beach above high water line	Blamires et al. 2003; Bannister et al. 2016
31	Greenhill Island, Northern Territory, Australia	Flatback (*Natator depressus*)	In front of vegetation	Hope and Smit 1998
32	Rancho Nuevo, Mexico	Kemp's ridley (*Lepidochelys kempii*)	In front of vegetation	Márquez 1994
33	Padre Island, Texas, USA	Kemp's ridley (*Lepidochelys kempii*)	In front of vegetation	Culver et al. 2020

CHAPTER FIVE: Supplementary Information

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Table S5.1. Year of study, nest ID, curved carapace length (CCL) measurements, clutch and excavation counts (including hatched, unhatched, predated eggs, and number of eggs removed from the nest).

Year	Nest ID	CCL cm	Clutch count	Total Excavation	Total hatched eggs	Predated eggs with holes	Undeveloped	Removed
2021	A14C	111	94	NA	NA	NA	NA	NA
2021	A15C	124	140	NA	NA	NA	NA	NA
2021	A18C	99	74	NA	NA	NA	NA	NA
2021	A24C	103	93	NA	NA	NA	NA	NA
2022	2201	NA	NA	NA	NA	NA	NA	NA
2022	2202	103	NA	45	8	9	28	NA
2022	2203	95	74	9	9	0	0	65
2022	2204	107	140	59	59	0	0	81
2022	2205	110	98	92	90	0	2	6
2022	2206	104	138	133	27	0	106	5
2022	2207	115.5	148	NA	NA	NA	NA	NA
2022	2208	111	131	NA	NA	NA	NA	NA
2022	2209	116	156	147	118	14	15	9
2022	2210	109.5	148	136	132	2	2	12
2022	2211	115	129	121	118	1	2	8
2022	2212	107.5	146	NA	NA	NA	NA	NA
2022	2213	114.5	131	123	113	3	7	8
2022	2214	113	154	144	119	18	7	10
2022	2217	105.5	108	108	108	0	0	0
2022	2219	106	98	NA	NA	NA		
2022	2215	104	145	139	39	8	92	6
2022	2216	115.5	176	146	145	0	1	30
2022	2218	107.5	133	133	46	7	80	0
2022	2221	113	138	NA	NA	NA	NA	NA
2022	2223	119	148	NA	NA	NA	NA	NA
2022	Unmarked1	NA	NA	112	108	0	4	NA

2022	Unmarked2	NA	NA	128	128	0	0	NA

Table S5.2. Number of predated eggs observed on the sand surface removed from a sea turtle nest.

Number of predated eggs on sand surface
20
17
69
11
8
15
22
35
2
7
5
10
3
47
30
4
5
3
15
2
2
3
2
27
5

Table S5.3. Studies reporting predators of sea turtle nests around the world. Location, sea turtle species and predator species.

Number	Location	Sea turtle species	Predator	Reference
1	Diego Garcia, Chagos Archipelago	Green (*Chelonia mydas*)	Coconut crab (*Birgus latro*)	Current study
1	Diego Garcia, Chagos Archipelago	Green (*Chelonia mydas*)	Ghost crab (*Ocypode spp.*)	Current study
1	Diego Garcia, Chagos Archipelago	Green (*Chelonia mydas*)	Black rat (*Rattus rattus*)	Current study
1	Diego Garcia, Chagos Archipelago	Green (*Chelonia mydas*)	Strawberry hermit crab (*Coenobita perlatus*)	Current study
2	Boa Vista, Cape Verde	Loggerhead (*Caretta caretta*)	Ghost crab (*Ocypode cursor*)	Marco et al. 2015
3	Cousine Island, Seychelles	Hawksbill (*Eretmochelys imbricata*)	Ghost crab (*Ocypode cordimana*)	Hitchins et al. 2004b
4	Sunshine coast, Queensland, Australia	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*)	Red fox (*Vulpes vulpes*)	O'Connor et al. 2017
5	Wreck Rock, Queensland, Australia	Loggerhead (*Caretta caretta*)	Red fox (*Vulpes vulpes*)	Lei and Booth 2017b
5	Wreck Rock, Queensland, Australia	Loggerhead (*Caretta caretta*)	Yellow-spotted goanna (*Varanus panoptes*)	Lei and Booth 2017b
5	Wreck Rock, Queensland, Australia	Loggerhead (*Caretta caretta*)	Lace monitor (*Varanus varius*)	Lei and Booth 2017b
6	Wreck Rock, Queensland, Australia	Loggerhead (*Caretta caretta*)	Yellow-spotted goanna (*Varanus panoptes*)	Lei et al. 2017
7	Wreck Rock, Queensland, Australia	Loggerhead (*Caretta caretta*)	Yellow-spotted goanna (*Varanus panoptes*)	Lei and Booth 2017a
8	Cape York Peninsula, Australia	Flatback (*Natator depressus*); Olive ridley (*Lepidochelys olivacea*)	Dingo (*Canis lupus dingo*)	Nordberg et al. 2019
8	Cape York Peninsula, Australia	Flatback (*Natator depressus*); Olive ridley (*Lepidochelys olivacea*)	Goanna (*Varanus panoptes*)	Nordberg et al. 2019

8	Cape York Peninsula, Australia	Flatback (*Natator depressus*); Olive ridley (*Lepidochelys olivacea*)	Feral pig (*Sus scrofa*)	Nordberg et al. 2019
9	Cape York Peninsula, Australia	Flatback (*Natator depressus*); Olive ridley (*Lepidochelys olivacea*)	Feral pig (*Sus scrofa*)	Whytlaw et al. 2013
10	Northern Territory, Australia	Flatback (*Natator depressus*); Olive ridley (*Lepidochelys olivacea*)	Saltwater crocodile (*Crocodylus porosus*)	Whiting and Whiting 2011
11	Andaman archipelago, India	Leatherback (*Dermochelys coriacea*)	Asian water monitor (*Varanus salvator*)	Sivasundar and Devi Prasad 1996
12	Orissa coast, India	Olive ridley (*Lepidochelys olivacea*)	Ghost crab (*Ocypode ceratophthalma*)	Tripathy and Rajasekhar 2009
12	Orissa coast, India	Olive ridley (*Lepidochelys olivacea*)	Feral dog (*Canis familiaris*)	Tripathy and Rajasekhar 2009
12	Orissa coast, India	Olive ridley (*Lepidochelys olivacea*)	Striped hyena (*Hyaena hyaena*)	Tripathy and Rajasekhar 2009
12	Orissa coast, India	Olive ridley (*Lepidochelys olivacea*)	Jackal (*Canis aureus*)	Tripathy and Rajasekhar 2009
13	Nagapattinam coast, India	Olive ridley (*Lepidochelys olivacea*)	Domestic dog (*Canis familiaris*)	Bhupathy 2003
13	Nagapattinam coast, India	Olive ridley (*Lepidochelys olivacea*)	Jackal (*Canis aureus*)	Bhupathy 2003
14	Akyatan beach, Turkey	Green (*Chelonia mydas*)	Red fox (*Vulpes vulpes*)	Brown and Macdonald 1995
14	Akyatan beach, Turkey	Green (*Chelonia mydas*)	Jackal (*Canis aureus*)	Brown and Macdonald 1995
15	Fethiye, Dalyan and Dalaman beach, Turkey	Loggerhead (*Caretta caretta*)	Red fox (*Vulpes vulpes*)	Başkale and Kaska 2005
15	Fethiye, Dalyan and Dalaman beach, Turkey	Loggerhead (*Caretta caretta*)	Badger (*Meles meles*)	Başkale and Kaska 2005
16	Barbados, Caribbean, USA	Hawksbill (*Eretmochelys imbricata*)	Asian mongoose (*Herpestes javanicus*)	Leighton et al. 2011

17	Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Ghost crab (*Ocypode quadrata*)	Brost et al. 2015
17	Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Raccoon (*Procyon lotor*)	Brost et al. 2015
18	Hobe Sound National Wildlife Refuge, Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Raccoon (*Procyon lotor*)	Engeman et al. 2006
18	Hobe Sound National Wildlife Refuge, Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Armadillo (*Dasypus novemcinctus*)	Engeman et al. 2006
19	Barrier Islands of Georgia, USA	Loggerhead (*Caretta caretta*)	Feral pig (*Sus scrofa*)	Butler et al. 2020
19	Barrier Islands of Georgia, USA	Loggerhead (*Caretta caretta*)	Coyote (*Canis latrans*)	Butler et al. 2020
19	Barrier Islands of Georgia, USA	Loggerhead (*Caretta caretta*)	Raccoon (*Procyon lotor*)	Butler et al. 2020
20	Masonboro Island Reserve, North Carolina, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*)	Red fox (*Vulpes vulpes*)	Halls et al. 2018
20	Masonboro Island Reserve, North Carolina, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*)	Raccoon (*Procyon lotor*)	Halls et al. 2018
21	Canaveral National Seashore, Florida, USA	Loggerhead (*Caretta caretta*)	Raccoon (*Procyon lotor*)	Welicky et al. 2012
22	Cayo Costa and North Captiva, Florida, USA	Loggerhead (*Caretta caretta*)	Raccoon (*Procyon lotor*)	Engeman et al. 2010
23	Canaveral National Seashore, Florida, USA	Loggerhead (*Caretta caretta*)	Raccoon (*Procyon lotor*)	Ratnaswamy et al. 1997

24	North Island, South Carolina, USA	Loggerhead (*Caretta caretta*)	Feral pig (*Sus scrofa*)	Engeman et al. 2019
25	South Carolina, USA	Loggerhead (*Caretta caretta*)	Coyote (*Canis latrans*)	Lamarre-DeJesus and Griffin 2015
26	Melbourne beach, Florida, USA	Loggerhead (*Caretta caretta*)	Ghost crab (*Ocypode quadrata*)	Bouchard and Bjorndal 2000
27	Cape San Blas, northwest Florida, USA	Loggerhead (*Caretta caretta*)	Red fire ant (*Solenopsis invicta*)	Parris et al. 2002
28	Palm Beach County, Florida, USA	Loggerhead (*Caretta caretta*)	Red fire ant (*Solenopsis invicta*)	Wetterer et al. 2014
28	Palm Beach County, Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Tropical fire ant (*Solenopsis geminata*)	Wetterer et al. 2014
28	Palm Beach County, Florida, USA	Green (*Chelonia mydas*); Loggerhead (*Caretta caretta*); Leatherback (*Dermochelys coriacea*)	Little fire ant (*Wasmannia auropunctata*)	Wetterer et al. 2014
29	Key Biscayne, Florida, USA	Loggerhead (*Caretta caretta*)	Click beetle (*Lanelater sallei*) larvae	Donlan et al. 2004
30	Texas, USA	Kemp's ridley (*Lepidochelys kempii*)	Coyote (*Canis latrans*)	Shaver 2020
30	Texas, USA	Kemp's ridley (*Lepidochelys kempii*)	Ghost crab (*Ocypode quadrata*)	Shaver 2020
31	Playa Cuixmala, Jalisco, Mexico	Olive ridley (*Lepidochelys olivacea*)	Ghost crab (*Ocypode quadrata*)	Garcıía et al. 2003
31	Playa Cuixmala, Jalisco, Mexico	Olive ridley (*Lepidochelys olivacea*)	Coati (*Nasua nasua*)	Garcıía et al. 2003
32	Corozalito, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Raccoon (*Procyon lotor*)	Espinoza-Rodríguez et al. 2023)
32	Corozalito, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Hermit crab	Espinoza-Rodríguez et al. 2023)

32	Corozalito, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Coati (*Nasua nasua*)	Espinoza-Rodríguez et al. 2023)
32	Corozalito, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Black vulture (*Coragyps atratus*)	Espinoza-Rodríguez et al. 2023)
33	Tortuguero, Costa Rica	Green (*Chelonia mydas*)	Coati (*Nasua nasua*)	Fowler 1979
33	Tortuguero, Costa Rica	Green (*Chelonia mydas*)	Black vulture (*Coragyps atratus*)	Fowler 1979
33	Tortuguero, Costa Rica	Green (*Chelonia mydas*)	Turkey vulture (*Cathartes aura*)	Fowler 1979
33	Tortuguero, Costa Rica	Green (*Chelonia mydas*)	Dog (*Canis familiaris*)	Fowler 1979
34	Ostional, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Black vulture (*Coragyps atratus*)	Burger and Gochfeld 2014
34	Ostional, Costa Rica	Olive ridley (*Lepidochelys olivacea*)	Dog (*Canis familiaris*)	Burger and Gochfeld 2014
35	Southern Bahia, Brazil	Loggerhead (*Caretta caretta*); Olive ridley (*Lepidochelys olivacea*); Hawksbill (*Eretmochelys imbricata*)	Dog (*Canis familiaris*)	Siqueira-Silva et al. 2020
36	Southern Bahia, Brazil	Loggerhead (*Caretta caretta*); Olive ridley (*Lepidochelys olivacea*); Hawksbill (*Eretmochelys imbricata*)	Domestic dog (*Canis familiaris*)	Nayelli Rangel Aguilar et al. 2022
36	Southern Bahia, Brazil	Loggerhead (*Caretta caretta*); Olive ridley (*Lepidochelys olivacea*); Hawksbill (*Eretmochelys imbricata*)	Red fox (*Vulpes vulpes*)	Nayelli Rangel Aguilar et al. 2022
37	Trindade Island, Brazil	Green (*Chelonia mydas*)	Feral pig (*Sus scrofa*)	Pereira et al. 2023
38	Trindade Island, Brazil	Green (*Chelonia mydas*)	Yellow crab (*Johngarthia lagostoma*)	de Faria et al. 2022
39	Amana natural reserve, French Guiana	Leatherback (*Dermochelys coriacea*)	Mole cricket (*Gryllotalpa gryllotalpa*)	Maros et al. 2003

40	Bijagos archipelago, Guinea-Bissau	Green (*Chelonia mydas*)	Nile monitor (*Varanus niloticus*)	Sampaio et al. 2022

CHAPTER SIX: Supplementary Information

Camera trapping: A novel approach to assess population estimates of nesting sea turtles

This work is a manuscript in preparation for Methods Ecol Evol as:

Stokes HJ, Hays GC, Esteban N. Camera trapping: A novel approach to assess population estimates of nesting sea turtles

Camera traps were set up on vegetation (e.g., *Cocos nucifera*; *Tournefortia*; Fig. S6.1a) pointing down the length of beach where possible or slightly towards the sea depending on vegetation obstruction (Fig. S6.1b). The distance observed from each camera trap was measured by creating 'turtle tracks' in the sand every 5m until the tracks were no longer visible in the camera trap images (range from a single camera trap = 5-30 m). HJS stood at each camera trap and recorded how many 'turtle tracks' were visible on the beach and analysed the images to record the number of tracks visible from the images (Fig. S6.1b).

Figure S6.1. Camera trap setup and example image from the camera trap**. a)** Camera trap set up and position (Model: Apeman H70) on the turtle nesting index beach in Diego Garcia, Chagos Archipelago. **b)** Image of 'turtle tracks' created in the sand at 5m intervals to determine the distance of view from each camera trap.

CHAPTER SEVEN: Supplementary Information

Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species

This work was published as:

Stokes HJ, Mortimer JA, Laloë J-O, Hays GC, Esteban N (2023) Synergistic use of UAV surveys, satellite tracking data, and mark-recapture to estimate abundance of elusive species. Ecosph 14:e4444. https://doi.org/10.1002/ecs2.4444

Table S7.1. Summary of studies reporting immature hawksbills density and abundance estimates. Habitat type: Seagrass (SG), Sponge (SP), Coral Reef (CR), Algae (A), Hard Bottom (HB), Patch Reef (PR), Rocky Reef (RR). The report date is used and in parentheses where study period is not recorded. NR (Not reported), MTN (Marine Turtle Newsletter). CMR (Capture Mark Recapture). Catch Per Unit Effort (CPUE) studies are not included.

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
1	Atlantic Ocean	Northwest Atlantic (Key West, Florida, USA) *All sites combined*	2003-2012	SG; SP HB; Intertidal flats; PR	Mean = 46.7 ± 11.3 SD	Transect	1.8 *0.6-5.3*	129	231	Journal	Herren et al. 2018
2	Atlantic Ocean	Gulf of Mexico (Rio Lagartos Sea Turtle Sanctuary, Yucaton, Mexico)	1998-1999	Octocorals (40-65% cover), S, HB, A, SG, SP, S, calcareous floor, rocks	Juvenile (NR)	Capture locations & habitat maps (GIS layers)	30	NR	NR	Journal	Cuevas et al. 2007
2	Atlantic Ocean	Gulf of Mexico (Rio Lagartos Sea Turtle Sanctuary, Yucaton, Mexico)	1998-1999	Octocorals (20-40% cover), S, HB, A, SG, SP, S, calcareous floor, rocks	Juvenile (NR)	Capture locations & habitat maps (GIS layers)	38	NR	NR	Journal	Cuevas et al. 2007

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
3	Atlantic Ocean	Caribbean Sea (Doce Leguas, Cuba)	(2000)	CR	Juvenile (NR)	Transect	122	NR	NR	Report	ROC 2000
3	Atlantic Ocean	Caribbean Sea (Doce Leguas, Cuba)	(2000)	CR	Juvenile (NR)	Transect	280	NR	NR	Report	ROC 2000
4	Atlantic Ocean	Caribbean Sea (Isle of Youth, Cuba)	(2000)	CR, S, SG, RR	NR	Transect	59	NR	NR	Report	ROC 2000
5	Atlantic Ocean	Caribbean Sea (Playa Norte, Dominican Republic)	1998	Sparse HB	Range = 19.5-69.7	Transect	5.6	NR	NR	Journal	Leon & Diez, 1999
6	Atlantic Ocean	Caribbean Sea (B. de las Aguilas, Dominican Republic)	1997	Sparse HB	Range = 19.5-69.7	Transect	6.6	NR	NR	Journal	Leon & Diez, 1999
7	Atlantic Ocean	Caribbean Sea (Cabo Rojo,	1997	Sparse HB	Range = 19.5-69.7	Transect	8.2	NR	NR	Journal	Leon & Diez, 1999

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
		Dominican Republic)									
8	Atlantic Ocean	Caribbean Sea (Los Frailes, Dominican Republic)	1997	CR	Range = 19.5-69.7	Transect	58.3	NR	NR	Journal	Leon & Diez, 1999
9	Atlantic Ocean	Caribbean Sea (Colita, Dominican Republic)	1998	CR	Range = 19.5-69.7	Transect	96.8	NR	NR	Journal	Leon & Diez, 1999
10	Atlantic Ocean	Caribbean (Mona Reef, Puerto Rico)	1992-2000	CR	Range = 20-84.5	CMR	24.1	NR	NR	Journal	Diez & van Dam, 2002
11	Atlantic Ocean	Caribbean Sea (Mona cliff wall, Puerto Rico)	1992-2000	Cliff wall	Range = 20-84.5	CMR	28.6	NR	NR	Journal	Diez & van Dam, 2002
12	Atlantic Ocean	Caribbean Sea (Monito cliff wall, Puerto Rico)	1992-2000	Cliff wall	Range = 20-84.5	CMR	120	NR	NR	Journal	Diez & van Dam, 2002
13	Atlantic Ocean	Caribbean Sea (Glover's	Apr 2007	Shallow lagoon; CR,	Mean = 43.2 ±	CMR	NR	22	1014 *105-1924*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
		Reef Marine Reserve, Belize)		SG, A; surveyed along forereef	0.62 SE; range = 20.0–75.1; n = 214						
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Sep 2007	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1141 *113-2395*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2008	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1438 *227-2649*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Jul 2008	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1307 *569-2045*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Nov 2008	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1636 *748-2523*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2009	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1319 *599-2039*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Nov 2009	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1652 *663-2641*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2010	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1;	CMR	NR	22	2159 *914-3405*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
					n = 214						
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Nov 2010	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1671 *776-2566*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Mar 2011	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1713 *792-2635*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2012	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	CMR	NR	22	1453 *604-2302*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2013	Shallow lagoon; CR, SG, A; surveyed	Mean = 43.2 ± 0.62 SE; range =	CMR	NR	22	1673 *531–2816*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
				along forereef	20.0–75.1; n = 214						
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2009	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	62.22 *39.63-97.69*	22	1618 *1030-2540*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Nov 2009	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	40.88 *29.27-57.10*	22	1063 *761-1485*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2010	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	55.12 *37.10-81.86*	22	1433 *965-2129*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Nov 2010	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	48.22 *32.57-71.41*	22	1254 *847-1857*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Mar 2011	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214	Transect	43.22 *30.45-61.33*	22	1124 *792-1594*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
					Results from captures						
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2012	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	25.21 *18.63-34.11*	22	555 *410-750*	Journal	Strindberg et al. 2016
13	Atlantic Ocean	Caribbean Sea (Glover's Reef Marine Reserve, Belize)	Apr 2013	Shallow lagoon; CR, SG, A; surveyed along forereef	Mean = 43.2 ± 0.62 SE; range = 20.0–75.1; n = 214 *Results from captures*	Transect	52.98 *39.80-70.53*	22	1166 *876-1552*	Journal	Strindberg et al. 2016

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
14	Atlantic Ocean	Southwest Atlantic (Arraial do Cabo, Rio de Janeiro, Brazil)	2019	CR	Juvenile (NR)	Transect	1e-10	NR	NR	Journal	Mello-Fonseca et al. 2021
15	Indian Ocean	Southwest Indian (Mahebourg Bay, Mauritius)	2013-2014	CR	NR	Transect	0.20	25	5	MTN	Reyne et al. 2017
15	Indian Ocean	Southwest Indian (North, Mauritius)	2013-2014	CR	NR	Transect	0.40	17	7	MTN	Reyne et al. 2017
15	Indian Ocean	Southwest Indian (Grand Bay-Port Louis, Mauritius)	2013-2014	CR	NR	Transect	0.88	80	70	MTN	Reyne et al. 2017

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
16	**Indian Ocean**	**Southwest Indian (Turtle Cove, Diego Garcia, Chagos Archipelago)**	**1996-2021**	**Shallow rocky tidal creeks: A HW**	**Mean = 46.9 ± 9.5 SD; range = 29.7-75.8; n = 227**	**CMR satellite tracking**	**241 (202-280)**	**1.28 (HW)**	**308 (258-358)**	**Journal**	**Present study**
16	**Indian Ocean**	**Southwest Indian (Turtle Cove, Diego Garcia, Chagos Archipelago)**	**1996-2021**	**Shallow rocky tidal creeks: A MW**	**Mean = 46.9 ± 9.5 SD; range = 29.7-75.8; n = 227**	**CMR satellite tracking**	**335 (280-389)**	**0.92 (MW)**	**308 (258-358)**	**Journal**	**Present study**
16	**Indian Ocean**	**Southwest Indian (Turtle Cove, Diego Garcia, Chagos Archipelago)**	**1996-2021**	**Shallow rocky tidal creeks: A LW**	**Mean = 46.9 ± 9.5 SD; range = 29.7-75.8; n = 227**	**CMR satellite tracking**	**454 (379-526)**	**0.68 (LW)**	**308 (258-358)**	**Journal**	**Present study**

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^{2})	Study site abundance *CI 95% / ±SE*	Publication type	Authors
17	Indian Ocean	Southeast (Zone C, West Island, Cocos & Keeling Island)	2004	Shallow lagoon: No habitat survey but mentions SG, A, CR	Mean = 57.6 ± 13 SD; range = 24.8–86.7 cm; n = 950 *Includes adults and immatures*	Transect	10.5	4.52	47 *± 25*	Journal	Whiting et al. 2014
17	Indian Ocean	Southeast (Zone E, South Island, Cocos & Keeling Island)	2004	Shallow lagoon: No habitat survey but mentions SG, A, CR	Mean = 57.6 ± 13 SD; range = 24.8–86.7 cm; n = 950 *Mainly immatures*	Transect	11.7	2.50	29.3 *± 29.3*	Journal	Whiting et al. 2014

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
17	Indian Ocean	Southeast (Zone F, South Island, Cocos & Keeling Island)	2004	Shallow lagoon: No habitat survey but mentions SG, A, CR	Mean = 57.6 ± 13 SD; range = 24.8–86.7 cm; n = 950 *Mainly immatures*	Transect	7.2	2.32	17 *± 10.6*	Journal	Whiting et al. 2014
17	Indian Ocean	Southeast (Zone E, South Island, Cocos & Keeling Island)	2005	Shallow lagoon: No habitat survey but mentions SG, A, CR	Mean = 57.6 ± 13 SD; range = 24.8–86.7 cm; n = 950 *Mainly immatures*	Transect	23	2.50	57 *± 30*	Journal	Whiting et al. 2014
17	Indian Ocean	Southeast (Zone F, South Island, Cocos & Keeling Island)	2005	Shallow lagoon: No habitat survey but mentions SG, A, CR	Mean = 57.6 ± 13 SD; range = 24.8–86.7 cm; n = 950	Transect	42	2.32	97 *± 44*	Journal	Whiting et al. 2014

	Ocean basin	Study location	Study period	Habitat	Size (straight carapace length, cm)	Method	Density (turtles km^{-2}) *95% CI*	Study site area (km^2)	Study site abundance *CI 95% / ±SE*	Publication type	Authors
					Mainly immatures						
18	Pacific Ocean	Southwest Pacific (Heron Reef, Queensland, Australia)	1969-1988	CR, A, SG	Range = 35-87.5; majority immature with range = 40-75	CMR	3.3	28.12	Mean annual resident population of 94 *± 50*	Journal	Limpus, 1992

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CHAPTER EIGHT: Supplementary Information

Assessing the impact of satellite tagging on growth rates of immature sea turtles

This work has been submitted to Methods Ecol Evol as:

Stokes HJ, Stokes KL, Mortimer JA, Laloë J-O, Esteban N, Hays GC. Assessing the impact of satellite tagging on growth rates of immature sea turtles

We plotted straight carapace length notch-tip against curved carapace length notch-tip to identify outliers that were removed from the growth rates dataset (where residual values from the linear model were > 2 cm; *N* = 9 out of 310) and confirm the statistically significant linear relationship ($R^2 = 0.99$; $N = 196$; $F_{1,194} = 26370$; $P < 0.001$) between the two measurements at Turtle Cove, Diego Garcia, Chagos Archipelago.

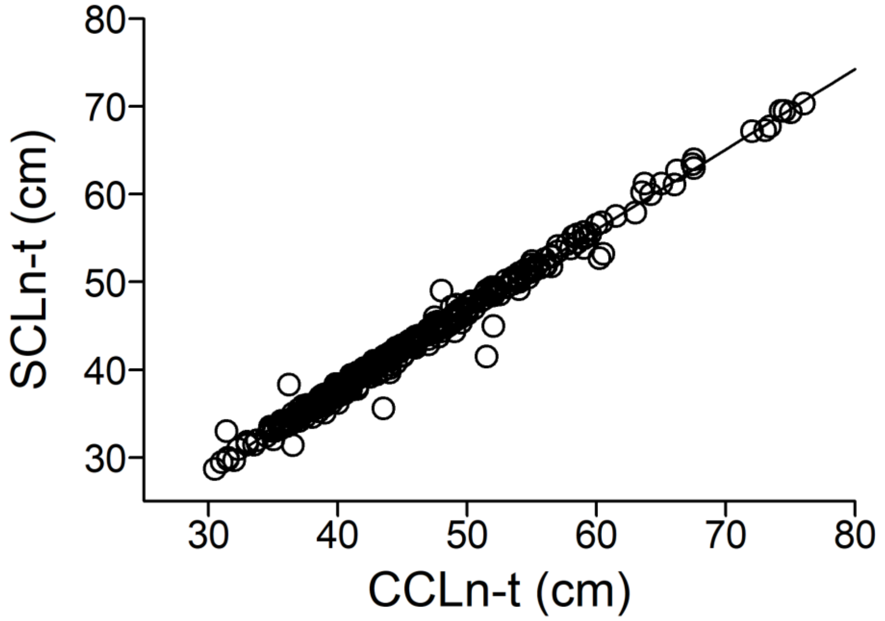

Figure S8.1. Straight carapace length notch-tip and curved carapace length notch-tip have a strong positive linear relationship (SCLn-t = 0.978 + 0.918*CCLn-t; $R^2 = 0.99$; $N = 196$; $F_{1,194} = 26370$; $P < 0.001$). The figure shows 310 points including repeated measurements from the same individuals. Repeated measurements were removed to fit and test the linear relationship.

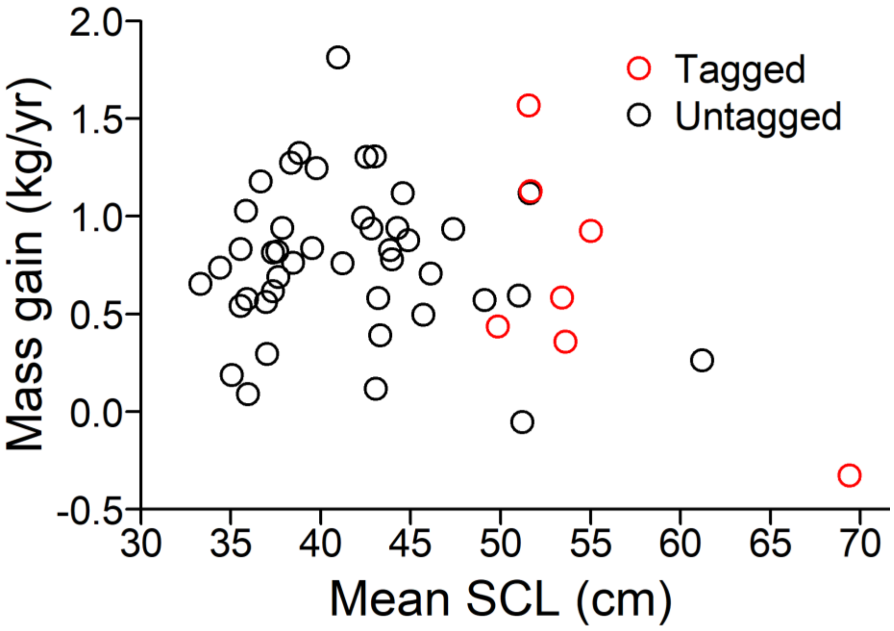

Figure S8.2. A comparison of mass gain against mean straight carapace length (SCLn-t) showed no relationship for tagged and untagged turtles. Data were calculated from the initial and recapture measurements of 50 juvenile hawksbill turtles at Turtle Cove, Diego Garcia.

Papers that I have co-authored during this thesis

Stokes KL, Esteban N, Stokes HJ, Hays GC (2023) High dive efficiency in shallow water. Mar Biol 170:45. https://doi.org/10.1007/s00227-023-04179-3

Conference presentations and seminars

International Sea Turtle Symposium March 2024, Thailand, Pattaya.

- Oral and poster presentation accepted.
- Member of the student committee.

International Sea Turtle Symposium March 2022, online.

- Oral: 'Density estimates of immature foraging turtles assessed by UAV surveys.'

Swansea University, 2023.

- Poster (selected by judges as one of 10) for the final round of the Swansea University wide competition: 'Using UAV surveys, satellite tracking and mark-recapture to estimate abundance of sea turtles.'

WEEN (Welsh Ecology and Evolution Network) 2020, online.

- Oral: 'Sea turtle ecology in the Chagos Archipelago'.

Demonstrating

- Bio111 (Botany and Ecology): Field support (sand dunes), lab support and marking.
- Bio252 (Stats and R): Marking.
- Bio112: Field support (rocky shore), lab support, marking.
- Bio 237 (Generation of barnacle larvae): Lab support.
- Bio 114 (Animal behaviour and biodiversity): Lab support.

Collaborations outside PhD research

- Sea turtle biopsies collected for genetic analysis.
- Satellite tagged immature and adult hawksbill and green turtles.
- Marine debris tracker app to record debris on sea turtle nesting beaches.

- Coral reef transects in the Chagos Archipelago.
- Contributions to supporting theories for archaeological finding of extinct turtle etc etc (cite paper in review)

Other

- 3-month PhD placement at Natural Resources Wales (November 2022 to February 2023).
- 2-month paid contract: Sea turtle foot patrol surveys in Saudi Arabia (June and August 2023).
- Presented our sea turtle research in the Chagos Archipelago to military personnel and local community of volunteers.
- Oversaw volunteer sea turtle activities in the Chagos Archipelago.
- Liaised with military personnel for fieldwork logistics on mainland and remote islands.
- Presented an overview of my PhD research to the Biosciences department students and staff members in 2020 and 2022.
- Article for Chagos News ‘Sea turtle ecology in the Chagos Archipelago’.