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SPATIAL BEHAVIOUR AND NESTING DYNAMICS OF GREEN TURTLES IN A WEST AFRICAN MARINE PROTECTED AREA

Cheila Sofia Ferreira Raposo

This thesis is submitted in partial fulfilment for the degree of PhD in

Behavioural Biology

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Thesis presented in fulfilment of the degree of PhD in Behavioural Biology, under the supervision of Paulo Catry, PhD., Professor at Ispa – Instituto Universitário de Ciências Psicológicas, Sociais e da Vida, presented at Ispa – Instituto Universitário de Ciências Psicológicas, Sociais e da Vida in the year of 2025.

This study was funded by Fundação para a Ciência e a Tecnologia through a doctoral grant (2020.08549.BD), and further supported by grants awarded to MARE (UIDB/04292/2020 and UIDP/04292/2020) and ce3c (UIDB/00329/2020) as well as a project granted to the Associate Laboratory ARNET (LA/P/0069/2020). Additional funding was provided by the MAVA Foundation and the Regional Partnership for Coastal and Marine Conservation (PRCM).

Fundação
para a Ciência
e a Tecnologia

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PORTUGUESA
EDUCAÇÃO, CIÊNCIA E INOVAÇÃO

ACKNOWLEDGEMENTS

I am deeply grateful to my supervisors – Ana Rita Patrício, Rui Rebelo and Paulo Catry – for their guidance and support throughout my PhD journey. I sincerely appreciate their willingness to accept me as their PhD student and give me the opportunity to conduct fieldwork in the João Vieira-Poilão Marine National Park. I am particularly thankful to Ana Rita Patrício and Rui Rebelo for their optimism and continued support, and to Paulo Catry for constantly encouraging me to do better.

This PhD was funded by the Fundação para a Ciência e a Tecnologia, Portugal, through a PhD grant (2020.08549.BD).

I express my gratitude to the Instituto da Biodiversidade e das Áreas Protegidas (IBAP), Dr. Alfredo Simão da Silva of Guinea-Bissau, for granting research permits and providing logistical assistance. I am especially thankful for the opportunity to have crossed paths with the IBAP’s technicians and rangers, and numerous Bijagós people. I am grateful to Tumbulo Bamba, Castro Barbosa and Aissa Regalla for their on-site assistance.

A warm thank you to Catarina Monteiro and Assana Camará, my travelling companions, who shared many hours of fieldwork with me and focused enthusiastically on fish sampling. I am also truly grateful to Seco Leão for his constant commitment and support throughout the fieldwork.

A special thank you to my partner João, who has learned so many new technological skills during this journey to support me. His invaluable contributions, enthusiasm and encouragement have been a central force throughout this journey.

A heartfelt thank you to my family. I am especially thankful to my mother for continuously believing in me, to my father for sharing my excitement about travelling to the Bijagós Archipelago, and to my sister who pushed me to pursue a career as a biologist. To my beloved grandparents, whose mid-way absence I came to deeply feel through this journey, I will be forever grateful for all their love, care, and guidance.

Palavras-chave:

Tartaruga-verde; distribuição espacial; desova; área marinha protegida

Key-words:

Green turtle; spatial distribution; nesting; marine protected area

Categorias de Classificação da tese

2200 Psychometrics & Statistics & Methodology

2260 Research Methods & Experimental Design

2400 Animal Experimental & Comparative Psychology

THE FOLLOWING CHAPTERS OF THIS THESIS HAVE BEEN PUBLISHED IN THE FOLLOWING INTERNATIONAL JOURNALS:

Chapter 2 – Raposo, C., Mestre, J., Rebelo, R., Regalla, A., Davies, A., Barbosa, C., & Patrício, A. (2023). Spatial distribution of inter-nesting green turtles from the largest Eastern Atlantic rookery and overlap with a marine protected area. *Marine Ecology Progress Series*, 703, 161-175. https://doi.org/10.3354/meps14225

Chapter 3 – Raposo, C., Rebelo, R., Catry, P., Ferreira-Airaud, M.B., Barbosa, C., Garcia, T.B., Regalla, A., Sampaio, M.S., & Patrício, A.R. (2024). Inter-island nesting dynamics and clutch survival of green turtles *Chelonia mydas* within a marine protected area in the Bijagós Archipelago, West Africa. *Marine Biology*, 171, 143. https://doi.org/10.1007/s00227-024-04463-w

Chapter 4 – Raposo, C., Patrício, A.R., Catry, P., Barbosa, C., Camará, A., Regalla, A., & Rebelo, R. (2025). Nutrient input from green turtle eggs and hatchlings in a West Africa Island and its nearshore environment. *Estuaries and Coasts*, 48, 64. https://doi.org/10.1007/s12237-025-01500-9

RESUMO

Compreender a distribuição espacial e a dinâmica de nidificação das tartarugas marinhas, um grupo carismático de megafauna marinha, é fundamental para a sua conservação, especialmente no caso de grandes populações que se concentram num único local de nidificação geograficamente restritivo e para as quais ainda existem lacunas de conhecimento. O Parque Nacional Marinho João Vieira e Poilão (doravante 'PNMJVP'), uma área marinha protegida localizada no sudeste do Arquipélago dos Bijagós, na Guiné-Bissau, abriga uma das maiores populações de tartarugas-verdes *Chelonia mydas* do mundo, sendo que a maior parte dos ninhos está concentrada na pequena e isolada ilha de Poilão. Nesta tese de doutoramento, avaliei parâmetros ecológicos essenciais da população de tartarugas-verdes do PNMJVP. Inicialmente, foquei-me nos movimentos de fêmeas reprodutoras no período entre desovas para investigar a sua distribuição espacial, fidelidade ao local e conexões entre ilhas do PNMJVP. De seguida, estimei o sucesso reprodutor na ilha de Poilão e nas restantes três principais ilhas do PNMJVP, com base na análise de dados previamente recolhidos sobre a sobrevivência dos ninhos e respetivas ameaças, como a predação e a inundação. Posteriormente, examinei o aporte de nutrientes proveniente dos ovos e tartarugas recém-eclodidas nas comunidades costeiras do PNMJVP. Para alcançar estes objetivos, foram utilizados vários métodos, como a marcação e o seguimento de tartarugas com recurso a anilhas e dispositivos de localização eletrónicos, respetivamente, e a quantificação de isótopos estáveis. Os resultados mostraram que as tartarugas-verdes permaneceram numa área restrita ao redor de Poilão durante o período entre desovas, com cerca de metade do seu território incluído na zona central de proteção integral do PNMJVP, demonstrando uma forte fidelidade aos locais de permanência entre desovas. A predação e a inundação dos ninhos de tartaruga-verde no PNMJVP foram mais elevadas nas ilhas adjacentes a Poilão, verificando-se um número limitado de conexões entre as principais ilhas do PNMJVP pelas tartarugas. Isto sugere uma possível dinâmica fonte-sumidouro, em que as ilhas com baixa produção de descendência funcionam como habitats sumidouros utilizados por indivíduos que migram de Poilão (fonte), que atualmente oferece as melhores condições para a sobrevivência dos ninhos. Localmente, as tartarugas-verdes contribuem com nutrientes para o ecossistema costeiro de Poilão, beneficiando principalmente as espécies localizadas diretamente nos locais de nidificação ou na sua proximidade. Por último, apresento a primeira revisão sobre o comportamento de fidelidade aos locais de reprodução e alimentação das tartarugas marinhas. Nesta revisão, identifico lacunas no conhecimento atual e destaco como a investigação científica no futuro pode abordar estas questões, além da necessidade de adotar um conceito padronizado de fidelidade ao local em estudos futuros. Esta tese contém dados sobre o comportamento e a ecologia das tartarugas-verdes no PNMJVP, que podem informar os gestores do parque sobre o planeamento espacial marinho e a priorização de esforços de conservação, de forma a apoiar a preservação das tartarugas marinhas.

ABSTRACT

Understanding the spatial distribution and nesting dynamics of sea turtles, a charismatic group of marine megafauna, is critical for their conservation. This is particularly important for some major sea turtle populations that aggregate at one specific geographically restricted nesting site and for which this knowledge remains incomplete. The João Vieira-Poilão Marine National Park (hereafter 'JVPMNP'), a marine protected area located southeast of the Bijagós Archipelago in Guinea-Bissau, hosts one of the world's largest green turtle *Chelonia mydas* breeding aggregations, but most of the nesting concentrates on the small and isolated island of Poilão. In this PhD thesis, I assessed key ecological parameters of the JVPMNP green turtle population. I first focused on the inter-nesting movements of breeding female green turtles to assess their spatial distribution, site fidelity, and inter-island linkages within the JVPMNP. Next, I estimated the reproductive success at Poilão and its 3 neighbouring islands within the JVPMNP, through the analyses of previously collected datasets on green turtle clutch survival and associated threats (predation and flooding). Following this, I examined the nutrient input from green turtle eggs and hatchlings into the coastal communities of the JVPMNP. To achieve these goals, several methods were employed, including sea turtle tagging and tracking, and the quantification of stable isotopes. Green turtles remained within a restricted area around Poilão during their inter-nesting intervals, with about half of their home range falling within the central no-take zone, and showing strong fidelity to inter-nesting sites. Clutch predation and flooding were higher on Poilão's neighbouring islands, with limited turtle exchanges between JVPMNP islands. This suggests a possible source-sink dynamic where islands with low reproductive output are sink habitats, used by migrants from Poilão (source), which currently offers the best conditions for clutch survival. On a local scale, green turtles contribute nutrients to the coastal ecosystem of Poilão, mainly benefiting species located directly at or in close proximity to sea turtle nesting sites. Lastly, I provide the first review of sea turtle breeding and foraging site fidelity, identifying gaps in the current knowledge and highlighting how future research can address these gaps, as well as the need for the adoption of a standardized concept of site fidelity in future studies. This work offers new insights into the behaviour and ecology of green turtles in the JVPMNP, providing valuable information to decision-makers for marine spatial planning and prioritizing conservation efforts, thereby supporting sea turtle conservation.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS AND NOTATIONS

Abbreviations

CCL	curved carapace length
IBAP	Instituto da Biodiversidade e das Áreas Protegidas
IN	inter-nesting
JVPMNP	João Vieira-Poilão Marine National Park
KUD	kernel utilization distribution
MPA	marine protected area
PIT	passive integrated transponder
PTT	platform terminal transmitter
SIA	stable isotope analysis
SLR	sea level rise

Notations

$\delta^{13}C$	carbon isotopic ratio
$\delta^{15}N$	nitrogen isotopic ratio

CHAPTER 1

GENERAL INTRODUCTION

Cheila Raposo

GENERAL INTRODUCTION

Marine megafauna, such as sea turtles, sharks, seabirds, and marine mammals, typically include species of high ecological value and conservation concern (Dulvy et al., 2021; Mazaris et al., 2017; Pimiento et al., 2020). These are often charismatic species (Albert et al., 2018), attracting public attention and increasing awareness of the importance to protect marine species and their habitats. Several species of marine megafauna are migratory (e.g., Hays, Mortimer, et al., 2014; Shaffer et al., 2006) and occupy geographic areas that are separated by hundreds or thousands of kilometres, crossing multiple jurisdictions and facing various anthropogenic threats (D. C. Dunn et al., 2019; Harrison et al., 2018; Lascelles et al., 2014). Therefore, protecting these species across their distribution range and at different stages of their migratory cycle is a scientifically and politically complex task (Lascelles et al., 2014).

Sea turtles, for example, perform periodic long-distance migrations between reproductive and non-reproductive sites (Luschi et al., 2003; P. Plotkin, 2003). Because sea turtles spend most of their lives at sea, studying them in their natural habitat is challenging. Nevertheless, some of their traits make it easier to locate them, as they tend to exhibit fidelity to foraging grounds (e.g., A. C. Broderick et al., 2007; Limpus & Limpus, 2001; Shimada et al., 2020), as well as to breeding grounds (e.g., Esteban et al., 2015; Mortimer & Portier, 1989; Shimada et al., 2021). These animals have an unescapable link to terrestrial habitats where they lay their clutches (Ackerman, 1997). This ability to cross the gap between marine and terrestrial habitats makes them carriers of nutrients from the marine realm to coastal sandy beaches where they nest (Lovich et al., 2018).

Historically, sea turtle research has seen a rising trend (Mazaris et al., 2018), providing new insights into sea turtle behaviour and ecology, such as where they nest, how frequently (intervals in days), which beaches they return to, their nesting beach site fidelity (Hays & Hawkes, 2018), and the threats they face (Fuentes et al., 2023; Rees et al., 2016). Nevertheless, essential data on such topics is still scarce in some important regions like West Africa.

1.1. SEA TURTLE EVOLUTION

The evolution of sea turtles is a notable example of adaptation to the marine habitat. The first turtles evolved more than 200 million years ago during the Late Triassic period, and the first fossils show clear aquatic affinities and are thought to reveal an adaptation to lacustrine/estuarine habitats (Evers & Benson, 2019). Several lineages since independently adapted to life in the marine habitat (Evers & Benson, 2019). The oldest known sea turtle fossil – *Desmatochelys padillai* – originated in the Lower Cretaceous period at least 120 millions years ago (Cadena & Parham, 2015). This fossil has an estimated length of 2 m and shows characteristics of the modern sea turtles (Cadena & Parham, 2015). Among the several sea turtle lineages, only the Chelonioidea clade, which includes modern sea turtles, has survived until the present (Evers & Benson, 2019). The Chelonioidea superfamily consists of 2 families, the Dermochelyidae and the Cheloniidae. The Dermochelyidae family (‘soft-shelled turtles’) includes a single species, the leatherback turtle *Dermochelys coriacea*, while the Cheloniidae family (‘hard-shelled turtles’) comprises 6 species: the flatback turtle *Natator depressus,* the green turtle *Chelonia mydas*, the loggerhead turtle *Caretta caretta*, the hawksbill turtle *Eretmochelys imbricata*, the olive ridley turtle *Lepidochelys olivacea*, and the Kemp’s ridley turtle *Lepidochelys kempii*. All 7 extant sea turtle species have adaptations to marine life, including flippers, hydrodynamic shells, ability to excrete salt through modified lachrymal glands, and cardiorespiratory adaptations to efficiently supply oxygen to tissues when diving (Ramos et al., 2020).

1.2. SEA TURTLE LIFE CYCLE

Sea turtles are long-lived and late-maturing reptiles (Heppell et al., 1999) with a life cycle that is shared by all species, with some interspecies differences. All species forage and nest in marine and terrestrial habitats, respectively, and migrate periodically throughout their lives to breed and forage (Lohmann, Luschi, et al., 2008). Breeding migrations typically range from 2 to 4 years (Southwood & Avens, 2010), varying according to species and population (e.g., Girondot & Fretey, 1996; Hawkes et al., 2005; Pendoley, Bell, et al., 2014; Shaver et al., 2016; Troëng & Chaloupka, 2007). After incubation, hatchlings enter the sea and undergo a developmental phase that lasts several years (commonly known as the ‘lost years’; Carr, 1986, 1987), after which they tend to settle in neritic or oceanic foraging grounds, depending on the species and population (Bolten, 2003). The juvenile turtles forage and continue to grow in these grounds until they reach sexual maturity (Musick & Limpus, 1997). This pattern is somewhat distinct across sea turtle species (Bolten, 2003). Flatback turtles are associated with type 1 (‘the neritic developmental pattern’), which refers to complete development in the neritic zone (Bolten, 2003). Hawksbill, green, loggerhead and some olive ridley turtle populations are often associated with type 2 ('the oceanic-neritic developmental pattern'), in which early juvenile development takes place in the oceanic zone and later juvenile development in the neritic zone (Bolten, 2003). Leatherback, Kemp's ridley and many olive ridley turtle populations are linked to type 3 ('the oceanic developmental pattern'), which involves entire development in the oceanic zone (Bolten, 2003). Following this developmental phase, mature female turtles will begin the cyclical breeding migrations between foraging and breeding grounds. Male turtles will also migrate periodically between foraging and mating grounds. During a single breeding season, female turtles lay successive clutches of eggs at species-dependent regular intervals, ranging from 2 to 3 weeks (N. J. Robinson et al., 2022). Between these successive nesting events, females remain in in-water sites (i.e., their inter-nesting habitats) that are often restricted to the vicinity of the nesting beach (e.g., Hamilton et al., 2021; K. M. Hart, Zawada, et al., 2013; Shimada et al., 2021; Tanabe, Cochran, & Berumen, 2023). Post-maturing, adult turtles have a long reproductive longevity of up to 10 (Kemp's ridley turtles; Avens et al., 2017), 22 (leatherback turtles; Avens et al., 2020), and 46 years (loggerhead turtles; Avens et al., 2015), with evidence suggesting that reproduction can occur until late in life.

1.3. ROLES OF SEA TURTLES

Sea turtles have had essential roles in sustaining the structure and function of marine ecosystems globally for over 100 million years. As keystone species, they are vital to support other species and preserve the function of ecological communities (Cottee-Jones & Whittaker, 2012). Their ecological roles range from entailing ecosystem dynamics as consumers, prey, and competitors, shaping community structure through top-down processes, acting as hosts for parasites and pathogens and substrates for epibionts, being biotic vectors of nutrients, and performing habitat modifications (Bjorndal & Jackson, 2003; Lovich et al., 2018). Top-down processes of green turtles are well described: grazing turtles are known to help maintain healthy seagrass meadows (Bjorndal, 1980; Heithaus et al., 2014), but high densities of turtles can lead to overgrazing (Christianen et al., 2014; Fourqurean et al., 2010, 2019) and reduce carbon sequestration (R. A. Johnson et al., 2017). Furthermore, sea turtles also play crucial ecological roles in terrestrial habitats (Bjorndal & Jackson, 2003; Lovich et al., 2018). Green and loggerhead turtle eggs can supply a high amount of marine-derived nutrients into nutrient-poor nesting beach environments (Bouchard & Bjorndal, 2000; Hannan et al., 2007; H. B. Vander Zanden et al., 2012), promoting vegetation growth and subsequent stabilization of coastal dune habitats (Moss, 2017).

Sea turtles also have recognised roles for human societies. They are used as food and trade products like turtle meat and eggs (Delisle et al., 2018; Hancock et al., 2017; Sardeshpande & MacMillan, 2019). Other trade products include tortoiseshell jewellery and oils used in traditional medicine. They can support ecotourism, that when effectively managed can avoid stressing the turtles while offering economic, educational and conservation benefits (Tisdell & Wilson, 2001; C. Wilson & Tisdell, 2001, 2003). Moreover, sea turtles are perceived as symbols, as illustrated by their inclusion in the coats of arms of the British Indian Ocean Territory, the Cayman Islands, and the Solomon Islands, and their depiction on coins and notes (Frazier, 2005). Another important social-related role acknowledged to sea turtles is their use as flagship species intended to engage public interest and gather support for conservation initiatives (Frazier, 2005). The cultural value of sea turtles can also facilitate adaptive governance, as observed in Torres Strait, Australia, where their value has resulted in co-management efforts between indigenous communities and government stakeholders (J. R. A. Butler et al., 2012).

1.4. THREATS TO SEA TURTLES

Sea turtles are a conservation-dependent group of animals due to several threats (Fuentes et al., 2023; Hamann et al., 2010; Rees et al., 2016), both natural and anthropogenic, that operate throughout their various life stages and habitats (Fuentes et al., 2023; Wallace, DiMatteo, et al., 2010; Wallace, Lewison, et al., 2010). Natural and anthropogenic threats include predation, direct take for use, diseases, pollution, climate change, bycatch, and coastal and marine development (Fuentes et al., 2023; Patrício et al., 2021). For example, predation can affect sea turtles in both marine and terrestrial habitats. While eggs, hatchlings and adult females are vulnerable to predators on nesting beaches (Gronwald et al., 2019; H. J. Stokes et al., 2024; Whiting & Whiting, 2011), hatchlings face predation as soon as they enter the sea (Bashir et al., 2020; Juhel et al., 2019; Tomás et al., 2010; P. Wilson et al., 2019). Immature and adult turtles may be at risk of predation and bycatch in oceanic areas (Aoki et al., 2023; Heithaus et al., 2008; Lewison & Crowder, 2007; Pitman & Dutton, 2004; Wallace et al., 2013). Climate-related threats can also affect sea turtles at nesting beaches, with rising incubation temperatures leading to increased embryo mortality (Hays et al., 2017; Howard et al., 2014; Pike, 2014) and extremely female-biased hatchling sex-ratios (Hays et al., 2017; Jensen et al., 2018; Monsinjon et al., 2019). Rising sea levels will reduce the available nesting areas (Fuentes et al., 2010) and increase clutch mortality due to seawater inundation (Varela et al., 2019). At sea, increasing seawater temperatures may shift the distribution range of sea turtles (Pikesley et al., 2015; Willis-Norton et al., 2015).

Recent research on the impact of these numerous natural and anthropogenic threats on sea turtles has identified key knowledge gaps and concerns about the impact and conservation strategies for each threat, and highlighted the need for a better understanding of the cumulative and synergistic effects of the aforementioned threats (Fuentes et al., 2023). For instance, bycatch and alteration of the terrestrial habitat were identified as primary threats in a multiple-threat study of the loggerhead turtle population in the southwest Atlantic Ocean (López-Mendilaharsu et al., 2020).

Globally, the anthropogenic-induced population declines in some sea turtle populations (Mazaris et al., 2017) have led to a decreased ability for these animals to fulfil their ecological roles (Bjorndal & Jackson, 2003). Nevertheless, balanced sea turtle populations can contribute to maintain healthy marine and terrestrial ecosystems, and these species continue to be culturally significant for many coastal communities. Despite threats, some sea turtle populations have recently experienced worldwide increases in the number of nests or nesting female abundance (Chaloupka et al., 2008; Hays, 2004; Hays et al., 2024), possibly reflecting positive trends resulting from conservation efforts (Hays et al., 2024; Mazaris et al., 2017).

1.5. SEA TURTLES IN THE JOÃO VIEIRA-POILÃO MARINE NATIONAL PARK, BIJAGÓS ARCHIPELAGO

The Bijagós Archipelago in Guinea-Bissau, West Africa, is identified as a globally and locally important region for green turtles (Catry et al., 2009; Patrício et al., 2019). The archipelago is not only regarded as a significant nesting site for sea turtles, but also as an exceptional site for the protection of other charismatic marine species, such as the West African manatee *Trichechus senegalensis* and the Atlantic humpback dolphin *Sousa teuszii*.

Located on the southeast of the Bijagós Archipelago, the João Vieira-Poilão Marine National Park (hereafter ‘JVPMNP’), is of particular relevance for sea turtles, thanks to its key green turtle breeding aggregation situated at Poilão Island. Poilão hosts the largest green turtle nesting population of the Bijagós Archipelago (Catry et al., 2002, 2009) and the second largest in the Atlantic (A. Broderick & Patrício, 2019), where an average of 25,000 clutches were laid each year between 2017 and 2021 (Catry et al., 2023). In addition to Poilão (43 ha), this 49,500 ha marine protected area (MPA) comprises 3 other main islands: João Vieira (900 ha), Meio (402 ha), and Cavalos (210 ha), and 3 small islets, of which some get covered by the high tide (Biai, 2018). These islands are covered by tropical forests and savannah, and surrounded by mangroves, rocky intertidal zones or sandy beaches. The climate is tropical and receives most of its annual rainfall from May to November due to the seasonal monsoon system. During the rest of the year rainfall is nearly absent. The major green turtle breeding season occurs from mid-June to mid-December, with the peak of the nesting activity in August and September, which largely coincides with the rainy season (Catry et al., 2002). Nevertheless, nesting has been documented throughout the year (Catry et al., 2009). Green turtle nesting is also observed at the other 3 main JVPMNP islands, but at incomparable lower numbers (Barbosa, Patrício, et al., 2018; Catry et al., 2002).

In addition to green turtles, hawksbills nest on the JVPMNP beaches (Barbosa, Patrício, et al., 2018). Apart from green and hawksbill turtles, other 3 sea turtle species (leatherback, loggerhead, and olive ridley turtles) are found in the JVPMNP waters (Barbosa, Patrício, et al., 2018). All of them can be found nesting within the Bijagós Archipelago, although leatherback and loggerhead turtles nest sporadically (Barbosa, Patrício, et al., 2018).

1.6. CONSERVATION CHALLENGES FOR SEA TURTLES IN THE JOÃO VIEIRA-POILÃO MARINE NATIONAL PARK, BIJAGÓS ARCHIPELAGO

The uninhabited, small and isolated island of Poilão has a sacred status perpetuated among the Bijagós traditional communities, who seldom visit it for social and religious ceremonies (Barbosa, Pires, et al., 2018; Catry et al., 2009). Additionally, beyond traditional restrictions, this island has been the focus of annual sea turtle monitoring campaigns since the year 2000 by the Instituto da Biodiversidade e das Áreas Protegidas (IBAP) of Guinea-Bissau, the governmental institution managing and monitoring biodiversity (Barbosa, Patrício, et al., 2018). Both factors have partly contributed to the effective long-term protection of green turtles at Poilão. However, the exposure to natural and anthropogenic threats may compromise the long-term sustainability of JVPMNP sea turtle populations and hinder their conservation outcomes.

One major conservation challenge at the JVPMNP is closely associated with the several threats to which turtles are subjected to, such as predation, direct take for use, climate change-related threats (flooding and coastal erosion), and bycatch (Barbosa, Patrício, et al., 2018; Catry et al., 2009). One of the biggest concerns currently is the use of adult female turtles and their eggs as food sources (Barbosa, Patrício, et al., 2018). Nevertheless, the remaining threats are also expected to have negative effects on green turtle clutch survival and overall population viability. For example, sea level rise (SLR) coupled with coastal erosion may significantly alter the available nesting area (Fuentes et al., 2010). During incubation, the successful development of embryos is subject to biotic (e.g., egg and clutch size, and predation) and abiotic (e.g., temperature, precipitation and flooding) factors (Chen et al., 2010; Fowler, 1979; Gravelle & Wyneken, 2022; Limpus et al., 2020; Wallace et al., 2004). Ultimately, these factors influence clutch survival and their overall reproductive success rates (Garrett et al., 2010; Veelenturf et al., 2022). Yet, essential data on green turtle clutch survival, reproductive success rates and associated threats are still lacking at the JVPMNP.

Other conservation challenges arise from a lack of knowledge about JVPMNP green turtle population spatial behaviour and nesting dynamics. How those female turtles are distributed while at sea remains poorly understood in most regions of the world, including the JVPMNP. This MPA's zonation establishes a central no-take zone and a buffer area with varying protection measures (Barbosa, Patrício, et al., 2018). In general, turtles are thought to remain within the limits of the MPA during inter-nesting intervals (i.e., the period between successive clutches within a single breeding season; Godley et al., 2010; Patrício et al., 2022). However, knowledge of the turtles' whereabouts or in-water site fidelity during inter-nesting intervals according to this zonation is scarce. Furthermore, the potential linkages between different islands of the JVPMNP, as well as the distribution of green turtle reproductive success across these islands, remain unknown. Addressing these conservation challenges may help inform conservation strategies and contribute to the long-term persistence of green turtles in the JVPMNP.

1.7. METHODS TO STUDY SEA TURTLE BEHAVIOUR AND ECOLOGY

Since the life cycle of sea turtles mostly occurs at sea, studying their behaviour can be challenging. Nevertheless, researchers have used a variety of methods to address key behavioural and ecological questions, contributing to sea turtle conservation. Among these, tagging, tracking and the quantification of stable isotopes have proven particularly relevant, and they closely align with the approaches used in this PhD thesis.

Tagging has been a worldwide essential resource for studying sea turtle behaviour and life history traits (A. C. Broderick & Godley, 1999). Tagging programs can individually identify turtles using external (flipper) or internal (passive integrated transponders, PIT) tags, or a mix of both. Usually, such programs rely on 2 external flipper tags or the combination of flipper and PIT tags to reduce tag loss (Omeyer et al., 2019). An earlier study showed that tagging has minimal effects on sea turtle nesting behaviour and reproductive success (A. C. Broderick & Godley, 1999), indicating that research involving tagging is unlikely to cause bias in scientific results. However, tagging only provides information on the initial tagging and subsequent resighting locations. To this regard, tracking has been proved useful for analysing sea turtle behaviour, including more detailed information on their distribution across space and time (Godley et al., 2008; Hays & Hawkes, 2018; Jeffers & Godley, 2016). The application of tracking devices has allowed to investigate the spatial distribution and movement patterns of sea turtles, as well as to identify important breeding grounds, foraging grounds and migratory corridors (K. Hart & Hyrenbach, 2009; Maxwell et al., 2011; Pendoley, Schofield, et al., 2014; Piacenza et al., 2018; K. L. Stokes et al., 2015). Furthermore, tracking data can be combined with fisheries data (e.g., geographic locations of fishing operations) to determine areas where turtles are more vulnerable (Howell et al., 2015), and with environmental data (e.g., sea surface temperature) to project shifts in the distribution of turtles due to water temperatures (Patel et al., 2021).

Stable isotope analysis (SIA) is another valuable tool for exploring sea turtle behaviour and ecology (Haywood et al., 2019). This method has been used to address sea turtle spatial, foraging and trophic research questions (e.g., Burgett et al., 2018; Ceriani et al., 2017; Dodge et al., 2011; Haywood et al., 2020; H. B. Vander Zanden et al., 2013), and is based on the fact that consumers' isotopic ratios reflect those of their dietary sources in reasonably predictable patterns (Fry, 2006). The most commonly used isotopes in sea turtle research are those of nitrogen (isotopic ratios: $^{15}N/^{14}N$, expressed as $\delta^{15}N$) and carbon (isotopic ratios: $^{13}C/^{12}C$, expressed as $\delta^{13}C$). While $\delta^{15}N$ gradually accumulates through the food chain and is thus used as an indicator of the consumer's trophic position, $\delta^{13}C$ changes little along the food chain and is usually used to trace the original sources of dietary carbon (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002). For instance, in terms of $\delta^{13}C$, there are differences between nearshore and offshore areas, as well as benthic and pelagic areas, with nearshore and benthic areas having higher primary productivity and thus higher $\delta^{13}C$ values, compared to the less productive offshore and pelagic areas, which have lower $\delta^{13}C$ values (Haywood et al., 2019). Stable isotope studies have therefore been mostly used to investigate sea turtle foraging ecology, focusing on identifying foraging grounds, revealing foraging site fidelity, and assessing diet (Haywood et al., 2019). At the Bijagós Archipelago, the isotopic signatures of juvenile green turtles indicated the continuous use of distinct foraging habitats (rocky vs. sandy) for long periods, and identified their dietary preferences (Madeira et al., 2022).

1.8. THESIS OVERVIEW

This thesis aimed to provide novel insights into the spatial distribution and nesting dynamics of green turtles within the JVPMNP, contributing to their conservation. Specifically, the work produced here involved assessing key ecological parameters, such as breeding and foraging site fidelity and plasticity, linkages between nesting sites, and reproductive success, to advance our understanding of (i) the movements of adult female turtles during their inter-nesting intervals as well as their fidelity to inter-nesting sites (Chapter 2), (ii) clutch survival and related threats, in addition to inter-island linkages within neighbouring islands of the

JVPMNP (Chapter 3), and (iii) the contribution of green turtle nutrients to the coastal and terrestrial ecosystems of the JVPMNP (Chapter 4). Additionally, this thesis aimed to compile and summarise, for the first time, the available information on sea turtle breeding and foraging site fidelity (Chapter 5).

This thesis is organised into 6 chapters. Chapter 1 provides the essential background. Chapters 2, 3, 4 and 5 are original research chapters and each focus on a specific topic, while Chapter 6 provides a general discussion of the findings and the main conclusions of the thesis. The topics of each of the 4 research chapters are as follows:

CHAPTER 2 – SPATIAL DISTRIBUTION OF INTER-NESTING GREEN TURTLES FROM THE LARGEST EASTERN ATLANTIC ROOKERY AND OVERLAP WITH A MARINE PROTECTED AREA

Marine spatial planning requires reliable spatial and ecological information. In Chapter 2, we investigated the inter-nesting movements of breeding female green turtles to determine their spatial distribution, site fidelity, and inter-island linkages within the JVPMNP. This information intends to guide national management on the effectiveness of this MPA's zonation in protecting the breeding green turtle population of Poilão.

CHAPTER 3 – INTER-ISLAND NESTING DYNAMICS AND CLUTCH SURVIVAL OF GREEN TURTLES *CHELONIA MYDAS* WITHIN A MARINE PROTECTED AREA IN THE BIJAGÓS ARCHIPELAGO, WEST AFRICA

Understanding how localised threats affect sea turtle reproductive success is critical for populations of conservation concern. In Chapter 3, we evaluated datasets on green turtle clutch survival and associated threats at Poilão, and 3 neighbouring islands within the JVPMNP, by estimating the total number of nests, quantifying clutch predation and flooding, and assessing hatching success at Poilão and one nearby island. This study seeks to identify suitable nesting sites (i.e., the island with best conditions for clutch survival), and provide recommendations to increase long-term clutch survival across the JVPMNP.

CHAPTER 4 – NUTRIENT INPUT FROM GREEN TURTLE EGGS AND HATCHLINGS IN A WEST AFRICA ISLAND AND ITS NEARSHORE ENVIRONMENT

Nutrient transport by animals can significantly affect primary productivity and biodiversity across multiple spatial scales. In Chapter 4, we examined the nutrient input from green turtle eggs and hatchlings into the coastal communities of the JVPMNP, comparing sites with low and high sea turtle nest densities and analysing the stable isotopes of pairs of organisms from the same species group – plants, crabs and fishes.

CHAPTER 5 – SEA TURTLE SITE FIDELITY: CURRENT KNOWLEDGE AND FUTURE DIRECTIONS

Knowledge of site fidelity is important for the successful conservation of highly mobile species because it allows us to identify key conservation areas and prioritize those to which these species return. To help guide future research, Chapter 5 provides a comprehensive overview of existing information on sea turtle site fidelity, including site fidelity to (i) nesting beaches, (ii) inter-nesting habitats, (iii) foraging grounds, and (iv) male site fidelity to breeding grounds.

CHAPTER 2

SPATIAL DISTRIBUTION OF INTER-NESTING GREEN TURTLES

SPATIAL DISTRIBUTION OF INTER-NESTING GREEN TURTLES FROM THE LARGEST EASTERN ATLANTIC ROOKERY AND OVERLAP WITH A MARINE PROTECTED AREA

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Published: (2023). Spatial distribution of inter-nesting green turtles from the largest Eastern Atlantic rookery and overlap with a marine protected area. *Marine Ecology Progress Series*, 703, 161-175. https://doi.org/10.3354/meps14225

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2.1. ABSTRACT

Understanding the spatial distribution of wildlife is fundamental to establish effective conservation measures. Tracking has been key to assess movement patterns and connectivity of sea turtles, yet some regions of great significance are largely understudied. We tracked 44 green turtles *Chelonia mydas* from the largest rookery in the Eastern Atlantic, on Poilão Island, Guinea-Bissau, during 2018 through 2020, to assess their inter-nesting movements, connectivity with nearby islands and fidelity to inter-nesting sites. Additionally, we investigated individual and environmental factors that may guide inter-nesting distribution and assessed the adequacy of a marine protected area to support this population during the breeding period. Green turtles had an overall home range of 124.45 km^2, mostly occupying a restricted area around Poilão Island, with 52% of this home range falling within the no-take zone of the João Vieira-Poilão Marine National Park. Turtles exhibited strong fidelity to inter-nesting sites, likely as a strategy to save energy. Only 2 turtles performed significant excursions out of the park, and connectivity between Poilão and nearby islands within the park was limited. Larger turtles and turtles tagged later in the nesting season tended to have smaller core areas and home ranges; thus, experienced breeders may be moving less and potentially benefit from energy saving. This study highlights the importance of a marine protected area for the conservation of one of the largest green turtle breeding populations globally, and provides suggestions for further increasing its effectiveness.

2.2. INTRODUCTION

Understanding the spatial distribution of a species is key to defining areas of conflict with human activities (Tuda et al., 2014) and establishing effective conservation measures (Allen & Singh, 2016; Fraser et al., 2018; Hays et al., 2019). For instance, the development of bio-logging technologies has enabled researchers to assess the spatial distribution and movement patterns of free-ranging marine species (Ropert-Coudert & Wilson, 2005), an essential step for the implementation of marine protected areas (MPAs; Hindell et al., 2020; Trathan et al., 2014).

Sea turtles, a group of charismatic species (K. L. Eckert & Hemphill, 2005; Veríssimo et al., 2012) of great ecological value (F. C. Coleman & Williams, 2002; León & Bjorndal, 2002; Pawlik et al., 2018), are considered as conservation-dependent due to worldwide population declines (Mazaris et al., 2017) and ongoing threats (Rees et al., 2016), although recent years have seen the recovery of some major populations (Chaloupka et al., 2008). Historically, most conservation efforts have been focused on the nesting beaches during the breeding season (Mazaris et al., 2017) to prevent poaching of female turtles and their eggs. However, the life cycle of sea turtles mostly occurs at sea, where they are subjected to targeted illegal fishing (Riskas et al., 2018), bycatch (López-Mendilaharsu et al., 2020), boat strikes (Shimada et al., 2017), habitat destruction (Goldberg et al., 2015) and plastic pollution (Roman et al., 2021).

Nowadays, tracking studies are widely used and contribute to our understanding of how sea turtles behave while at sea (Hays & Hawkes, 2018). Several tracking studies have focussed on post-breeding movements (Hays & Hawkes, 2018) and on the inter-nesting habitat of female turtles (e.g., Chambault et al., 2016; S. A. Eckert et al., 2006; Esteban et al., 2017; Godley et al., 2010; Hamilton et al., 2021; Schofield et al., 2009; Shimada et al., 2021; Zbinden et al., 2007), increasing our knowledge of their ecology and population connectivity. We know that during the breeding period females nest several times and may spend several months near nesting sites, incurring energy-costly activities such as mating, oogenesis, travelling to and from the nesting beaches, crawling on land and egg-laying (Chambault et al., 2016; Hamann et al., 2002, 2022). The inter-nesting interval corresponds to the period between successive clutches being laid by a turtle during a single breeding season (Hays, Broderick, et al., 2002; Price et al., 2019). In order to optimize their energy expenditure during the sequential inter-nesting intervals, green turtles *Chelonia mydas* have been shown to remain in the vicinity of nesting beaches (Blanco et al., 2013; Esteban et al., 2015; Waayers et al., 2011), resting on the seabed (Hays et al., 2000), or exhibiting assisted resting (i.e., remaining motionless at the seabed whilst aided by a structure, such as rocks; Fernandes et al., 2017; Reisser et al., 2013; Walcott et al., 2014). Sea turtles are mostly thought to fast during inter-nesting intervals (e.g., green turtles: Chambault et al., 2016; Hamann et al., 2002;

Page-Karjian et al., 2020; hawksbill turtles *Eretmochelys imbricata*: Goldberg et al., 2013; A. J. B. Santos et al., 2010; Walcott et al., 2012; leatherback turtles *Dermochelys coriacea*: Asada et al., 2022; Plot et al., 2013). Nevertheless, at sites where food is available, inter-nesting turtles may opportunistically feed, as observed for example among leatherback (Asada et al., 2022) and green turtles (Hays, Glen, et al., 2002; Richardson et al., 2013).

Tracking studies of breeding green turtles show that they tend to have small home ranges (Blanco et al., 2013; Chambault et al., 2016; K. M. Hart, Zawada, et al., 2013; K. M. Hart et al., 2017; Shimada et al., 2021; Snape et al., 2018). Yet, larger home ranges were also found for green turtle populations in Sri Lanka (Richardson et al., 2013) and in the Mediterranean Sea (Levy et al., 2017). Overlap between home ranges and MPAs during the breeding period has been assessed for several green turtle populations worldwide (Hamilton et al., 2021; Hays, Mortimer, et al., 2014; Revuelta et al., 2015), and tracking studies conducted during the breeding period have contributed to the designation and management of MPAs (T. M. Dawson et al., 2017).

The Bijagós Archipelago, in Guinea-Bissau, West Africa, hosts one of the largest nesting aggregations of green turtles worldwide (Catry et al., 2009; Patrício et al., 2019). Females nest on several islands of the archipelago, but the vast majority nest at Poilão Island (Catry et al., 2009). Two previous studies have shown that green turtles remain within the limits of the local MPA, the João Vieira-Poilão Marine National Park (hereafter 'JVPMNP'), during inter-nesting intervals (Godley et al., 2010; Patrício et al., 2022). However, no assessment has been made of the importance of the zones of the park – encompassing a central no-take zone and a buffer area subject to different protection measures – and no attempt has been made to explore individual and environmental aspects that may guide inter-nesting distribution.

Here, we analyse 3 years of tracking data from 59 female green turtles and evaluate their fine-scale movements during the breeding period. We assess their usage of the different zones of the JVPMNP, the fidelity to inter-nesting sites, and the connectivity between Poilão and the nearby JVPMNP islands. We explore how individual and extrinsic factors affect home ranges and core areas. This study will inform national management authorities on the suitability of the zonation of the JVPMNP for protecting this population, since this MPA was established in 2000 when no data on the inter-nesting distribution of turtles nesting at Poilão was available. It also provides novel information on the ecology of green turtles over the breeding period.

2.3. MATERIALS AND METHODS

2.3.1. STUDY SITE

Fieldwork was carried out at Poilão (10°52’N, 15° 43’ W; **Fig. 2.1**), an island surrounded by intertidal rocks and sandy areas, located in the southeast of the Bijagós Archipelago, Guinea-Bissau, West Africa (**Fig. 2.1A**). Together with 3 other main islands (João Vieira, Cavalos and Meio) and one islet (Cabras), Poilão is located within the JVPMNP (**Fig. 2.1B**). This MPA encompasses a central no-take zone (11,029 ha) where fishing activities are forbidden, and a peripheral zone (37,838 ha) where fishing is allowed to local residents and licensed recreational fishers using regulated equipment (**Fig. 2.1B**; see Patrício et al., 2022). With only 43 ha, Poilão hosts the largest green turtle nesting aggregation in the Bijagós Archipelago (Catry et al., 2002, 2009) and in the Eastern Atlantic (Patrício et al., 2019), with an annual average of 25,436 clutches (2013−2016; Patrício et al., 2019). Although nesting has been recorded year-round (Catry et al., 2009), a marked breeding season occurs from mid-June to mid-December, with a peak nesting activity between August and September (Catry et al., 2002). For the purpose of this study, the coastline of Poilão was divided in 4 sectors from west to east (FAR, AO, AE, CAB; see **Fig. 2.1C**). With the exception of AE, all beach sectors are characterized by the presence of a barrier of intertidal rocks.

2.3.2. TAG DEPLOYMENT

Satellite and archival tags were deployed on 59 female green turtles during the 2018, 2019 and 2020 breeding seasons, between August 13 and November 8. In 2018, 20 turtles were equipped with SPOT-375B tags (99 × 55 × 21 mm, 152 g, ®Wildlife Computers), which rely on the Argos satellite system only and have an accuracy of hundreds of meters to >1 km (Thomson et al., 2017). In 2019 and 2020, FastGPS tags (F6G 376B, 115 × 64 × 43.5 mm, 220 g, ®Lotek), which provide both Argos and GPS locations (mean ± SD accuracy of fast-acquisition GPS ranging from 172.0 ± 317.5 m for a minimum of 4 satellites to 26.0 ± 19.2 m for a maximum of 8 satellites; Hazel, 2009), were deployed on 9 and 15 females, respectively. In 2019, 15 additional turtles were equipped with Arribada Horizon GPS archival tags (Horizon version 3.95 × 64 × 32 mm, Arribada/Zoological Society of London), that provide GPS locations (mean ± SD horizontal accuracy: 12.05 ± 25.95 m) upon retrieval and download. SPOT-375B tags were not configured to provide haul-out data, and FastGPS and Arribada Horizon GPS tags were not fitted with a wet/dry sensor.

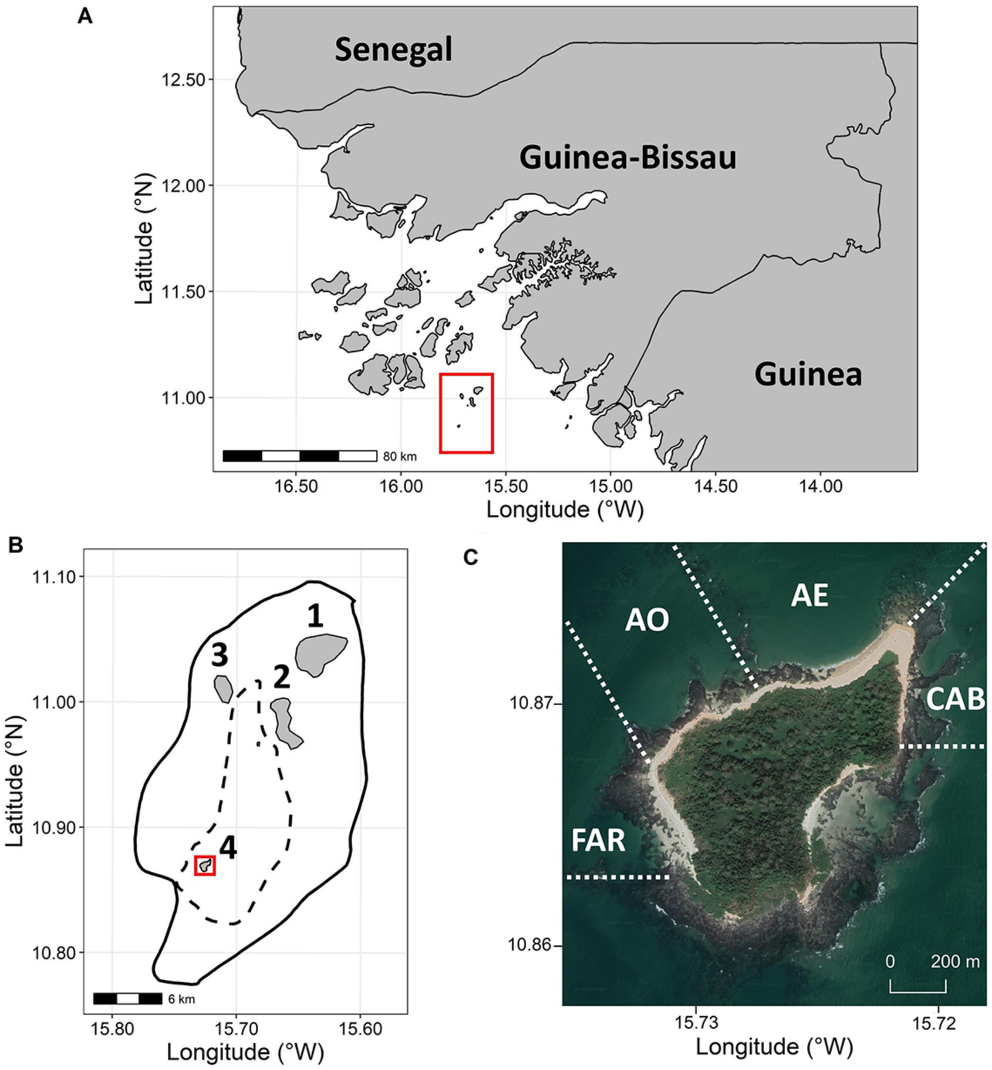

Fig. 2.1. (A) Location of the study area (red box) within the Bijagós Archipelago, Guinea-Bissau. **(B)** Close-up on the conservation areas. The peripheral solid black line and the central black dotted line depict the contours of the João Vieira-Poilão Marine National Park and the limit of the central no-take zone, respectively. The islands located within the park are João Vieira (1), Meio (2), Cavalos (3) and Poilão (4, red box). Cabras is an islet located southwest of Meio, at the limit of the no-take zone. **(C)** For the purpose of this study, Poilão's coastline was divided in 4 sectors from west to east (FAR, AO, AE, CAB)

Tag deployment occurred after oviposition had begun, and tracking devices were deployed within 20 min. Details of tag deployment can be found in **Protocol S2.1** in the Appendix. Turtles fitted with the tracking devices were identified by their satellite tag (platform terminal transmitter, PTT) number (**Table S2.1**). Although clutch frequency can be estimated through satellite tracking (Esteban et al., 2017), we did not attempt to estimate this parameter because tags were not deployed at the beginning of the breeding season.

Uniquely numbered self-piercing tags were applied on both front flippers, and curved carapace length (hereafter ‘CCL’) was measured from the base of the nuchal scute to the tip of the furthest marginal scute to the nearest 1 mm using a flexible measuring tape, according to standard biometry measurement procedures (Bolten, 1999). The beach sector where turtles were nesting was noted. Handling time was reduced to what was strictly necessary to minimize disturbance to turtles. All turtles maintained their nesting activity and returned safely to the sea.

2.3.3. TRACKING DATA PROCESSING

The breeding period was defined as the time from tag deployment until a turtle exhibited a directed movement away from Poilão with no return. Locations corresponding to post-nesting movements were discarded from analyses. The individuals for which tags had a low frequency acquisition (ca. one location per day) or with a recording duration shorter than 4 d were excluded from the dataset. Four days was selected as the minimum recording duration because this is half the minimum inter-nesting interval reported for green turtles in Poilão (mean ± SD: 12.2 ± 1.6 d, range: 8−17 d; Catry et al., 2009), and we observed that turtles tended to reach the maximum distance from their nesting site within 4 d. The retained tracks were processed and analysed using R v3.6.1 software (R Core Team, 2019).

The Argos tracking data were first filtered by removing the class Z locations, corresponding to the lowest location class provided by the Argos service (considered as error locations; Thomson et al., 2017; Witt et al., 2010). All GPS locations were obtained from at least 4 satellites. A speed filter of >5 km h^{-1} and an azimuth filter of <20° were applied to all tracks using the sdafilter function from the argosfilter R package (Freitas, 2012) to discard unrealistic fixes (Metcalfe et al., 2020). The McConnell speed filter (McConnell et al., 1992) was then executed with a 5 km h^{-1} threshold using the speedfilter function from the trip R package (Sumner, 2011; Sumner et al., 2009), to further remove implausible locations (Patterson et al., 2010). A Kalman filter was then fitted with the crwMLE function from the crawl R package (D. S. Johnson et al., 2008; D. S. Johnson & London, 2018), implementing error multiplication factors from the foiegras R package (Jonsen & Patterson, 2019), to increase estimates of positioning accuracy (Lopez et al., 2014; Patterson et al., 2010). Locations were interpolated at 2 h time steps, corresponding to the mean time interval between 2 raw consecutive locations, through the crwPredict function from the crawl R package (D. S. Johnson et al., 2008; D. S. Johnson & London, 2018). The original locations were not retained in the analyses (Calenge, 2006).

2.3.4. MOVEMENT PATTERNS, HOME RANGES, CORE AREAS AND OVERLAP WITH A MARINE PROTECTED AREA

The geoDist function from the oce R package (Kelley et al., 2019) was used to calculate, for each turtle position, the distance to the previous location and the distance to the tag deployment site. The distance to the nearest point of the coastline of each island of the JVPMNP was calculated by assessing the distance between each turtle location and custom island shapefiles obtained from Google Earth, using the st_distance function (sf R package; Pebesma, 2018). Bathymetry was obtained from the ETOPO1 (1-arc minute resolution) bedrock database (NOAA National Geophysical Data Center, 2009) and associated to each turtle location.

For each individual, the proportion of locations falling within the protected areas of the JVPMNP was assessed and kernel utilization distributions (KUDs) were calculated, using the kernelUD function from the adehabitat R package (Calenge, 2006), with a 1000 m smoothing parameter. This threshold was determined as the reference bandwidth computed by the function when including all individuals. KUDs of 50 and 95% were used to represent the core areas and home ranges, respectively (e.g., Hamilton et al., 2021).

The overall home range and core area were also assessed, as well as their overlap with the limits of the park and of the central no-take zone.

2.3.5. IN-WATER SITE FIDELITY

We aimed to determine whether female green turtles use the same in-water sites over a breeding season. To do this, we divided the tracks into inter-nesting intervals by identifying or estimating haul-out events. We then estimated the overlap of home ranges and core areas between inter-nesting intervals.

We selected all turtles with location data encompassing at least 2 complete theoretical inter-nesting intervals (i.e., recording duration >24 d; mean inter-nesting intervals = 12.2 d; Catry et al., 2009), and then randomly selected 2 of those intervals for each turtle. The areas (km^2) of the 50 and 95% KUDs were assessed for each interval as well as the overlap (%)

between the 2 intervals of the same turtle. The overlap was defined as the proportion of the second interval included in the first.

For a visual observation of in-water site fidelity over time, we plotted successive home ranges and core areas of 3 turtles for which we had the longest recording durations (encompassing more than 2 inter-nesting intervals) and the highest confidence on the nights of haul-out events. For these individuals, the inter-nesting intervals were clearly identified either through direct observations at the nesting beaches and/or by locations ashore or very close to shore between dusk and dawn compatible with the timing of a nesting event. For one of these turtles, we calculated the overlaps of home ranges and core areas over time, first using the estimates of the first inter-nesting interval as a reference (% of any following inter-nesting interval within the first inter-nesting interval) and then the estimates of the previous inter-nesting interval (% of inter-nesting interval ‘n’ in inter-nesting interval ‘n−1’).

2.3.6. CONNECTIVITY BETWEEN NESTING SITES

We inspected tracking data for movements close to other JVPMNP islands, indicative of possible nesting events. Additionally, we assessed flipper tag data collected between 2018 and 2020 from turtles observed nesting at Poilão and Meio islands to further evaluate potential connectivity between adjacent islands within the JVPMNP.

2.3.7. STATISTICAL ANALYSIS

A multiple linear model was first used to investigate the influence of the CCL, nesting beach sector, date of tag deployment (day-of-year), recording duration and year on the extent of the KUD areas. Because not all tag types were deployed each year (in 2018, only SPOT-375B tags were deployed), we cannot disentangle the effects of year and tag type in a general model. We thus performed 2 other models to independently test the effect of these 2 variables on the extent of the 50 and 95% KUDs. We investigated the year effect for turtles equipped with FastGPS tags in 2019 and 2020. We expected a higher competition for space around nesting sites in 2020 compared to 2019, since the number of emergences was much larger in that year (79,859 vs. 9,606 in 2019). We investigated the effect of the tag type in 2019, when both FastGPS and Arribada Horizon GPS tags were deployed.

The models included all individuals for which CCL measurements were available. All model prerequisites (absence of heteroscedasticity, multicollinearity and correlation) were verified, and continuous explanatory variables were centered and scaled prior to analyses. Models were backward selected with the Akaike information criterion (Akaike, 1998) using the stepAIC function (Venables & Ripley, 2002). The diagnostic plots of the models were visually inspected. If the model residuals were not adequate to enable model validation, outliers were discarded, and the model was fitted again. All descriptive statistics are presented as mean ± SD.

2.4. RESULTS

Of the 59 turtles equipped with tracking devices, 15 were excluded from spatial analyses due to tag failure or insufficient data. The remaining 44 turtles were tracked for 27.5 ± 21.5 d (range 4−82 d; **Table S2.1**); they travelled a horizontal distance of 182.7 ± 178.7 km (range <1−643.9 km), and their horizontal speed was 0.24 ± 0.16 km h^{-1} (range 0−0.65 km h^{-1}). These individuals remained within a distance of 3.5 ± 5.0 km (range <1−27 km) from their tagging sites and within 1.5 ± 0.2 km (range 0.1−18.2 km) from the coastline of any JVPMNP island, using very shallow areas ranging between 2.3 and 6.0 m deep (4.0 ± 0.9 m). Their CCL was 99.5 ± 8.8 cm (range 78.0−121.5 cm, *n* = 42; 2 individuals were not measured).

2.4.1. DISTRIBUTION OF TURTLES AND OVERLAP WITH A MARINE PROTECTED AREA

The inter-nesting habitats of individual turtles ranged from 4.36 to 54.06 km^2 (10.37 ± 7.96 km^2, *n* = 44) and 18.83 to 495.56 km^2 (79.63 ± 86.92 km^2, *n* = 44) for 50 and 95% KUDs, respectively (**Table S2.1**). The overall core area of turtles spanned over 10.85 km^2 and was entirely included within the JVPMNP for the duration of the tracking periods (**Fig. 2.2B**). An expressive majority (95%) of this core area was encompassed within the central no-take zone (**Fig. 2.2B**). The overall home range of these turtles spread over 124.45 km^2 (**Fig. 2.2B**), with 88 and 52% of the 95% KUD included within the limits of the JVPMNP and of the no-take zone, respectively (**Fig. 2.2B**). Individual turtles spent a considerable amount of time within the protected area, with 96.2 ± 10% of locations within the JVPMNP and 86.5 ± 14.5% of locations within the no-take zone (**Table S2.1**, **Fig. S2.1**).

The smallest tracked turtle (PTT60897; CCL = 78 cm) swam off the limits of the JVPMNP and the farthest from Poilão, and was discarded from the general linear model explaining the 50% KUD. Another individual that travelled out of the JVPMNP was discarded from the model explaining the 95% KUD: PTT60891 (CCL = 92.5 cm).

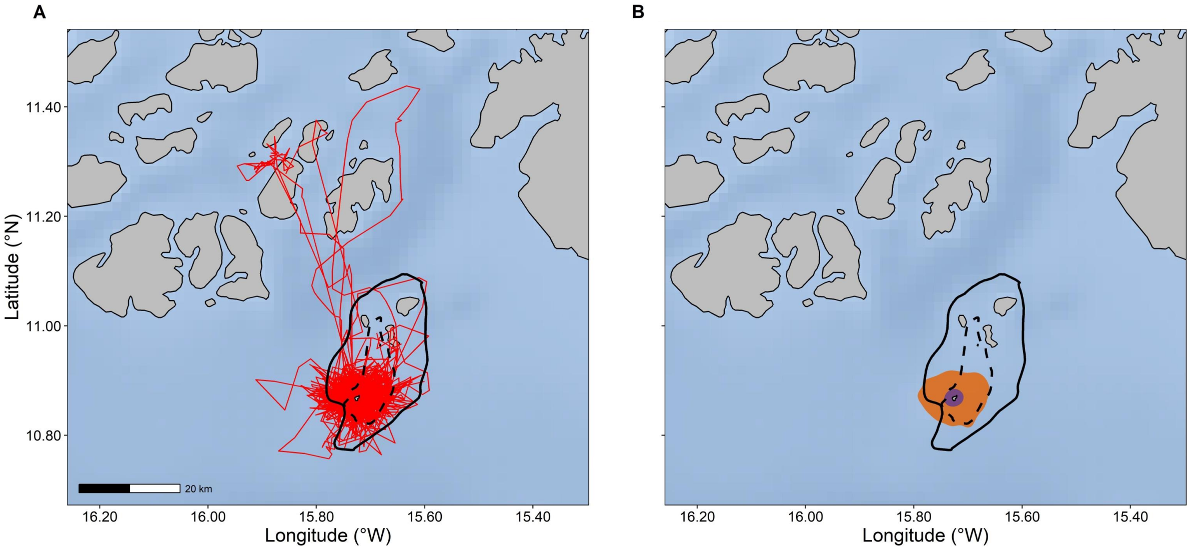

Fig. 2.2. Movements and estimated inter-nesting spatial distribution of 44 female green turtles tracked within the Bijagós Archipelago, Guinea-Bissau, over the 2018, 2019 and 2020 breeding periods. The dotted and solid black lines represent the contours of the no-take zone and of the João Vieira-Poilão Marine National Park, respectively. **(A)** The red lines show the tracks of female turtles. **(B)** The purple and orange areas depict their overall core area (50% kernel utilization distribution) and home range (95% kernel utilization distribution), respectively

All explanatory variables were kept during the stepwise model selection for the 50% KUD general model and explained approximately 37% of its variance (adjusted $r^2 = 0.37$, $n = 41$, $F_{8,32} = 3.9$, $p < 0.01$). Inter-nesting core areas increased significantly with the recording duration and were significantly smaller in 2019 compared to 2018 (**Tables 2.1** & **S2.2**). Turtle size had a marginally significant negative effect on core areas (**Table 2.1**). Lastly, core areas tended to decrease when tag deployment occurred later in the breeding season, but this effect was not significant (**Table S2.2**).

For the 95% KUD general model, CCL was dropped during the stepwise model selection. The remaining explanatory variables explained 30% of the variance (adjusted $r^2 = 0.30$, $n = 42$, $F_{7,34} = 3.5$, $p < 0.01$). As with core areas, home ranges were significantly larger for longer recording durations (**Tables 2.1** & **S2.2**). Turtles tended to display smaller home ranges in 2019 and larger ones in 2020 compared to 2018, and this effect was marginally significant (**Table 2.1**). Home ranges also tended to be smaller for late tag deployments and among turtles tagged at beach sectors surrounded by a rocky reef (all but AE; **Table S2.2**), but these effects were not significant.

Table 2.1. ANOVA table from the general multiple linear model predicting the extent of the 50% and 95% kernel utilization distribution (KUDs). **Bold** indicates significant values (*p* <0.05)

Response variables	Explanatory variables	df	SS	MS	F	*p*
50% KUD	CCL	1	38.75	38.75	3.23	0.08
	Nesting beach sector	3	64.51	21.50	1.79	0.17
	Date of tag deployment	1	16.45	16.45	1.37	0.25
	Recording duration	1	95.04	95.04	7.93	**<0.01**
	Year	2	160.21	80.11	6.69	**<0.01**
	Residuals	32	383.46	11.98	–	–
95% KUD	Nesting beach sector	3	6313.00	2104.50	1.58	0.21
	Date of tag deployment	1	80.00	80.30	0.06	0.81
	Recording duration	1	17949.00	17949.10	13.50	**<0.001**
	Year	2	8375.00	4187.50	3.15	0.06
	Residuals	34	45208.00	1329.60	–	–

In the model testing the effect of year (2019 vs. 2020), none of the explanatory variables had a significant effect on both 50% (*n* = 19, *p* = 0.15) and 95% KUDs (*n* = 19, all explanatory variables were dropped during the stepwise model selection).

There was no effect of tag type on 50% KUD in 2019; in fact, this variable was dropped during stepwise model selection (only CCL, date of tag deployment and recording duration were kept, explaining 34% of the variance: adjusted $r^2 = 0.34$, *n* = 19, $F_{3,15} = 4.2$, *p* <0.05; **Table S2.3**). All explanatory variables were kept in the model to test tag type effect on 95% KUD in 2019, accounting for 59% of the variance (adjusted $r^2 = 0.59$, *n* = 19, $F_{7,11} = 4.8$, *p* <0.05). However, tag type did not significantly affect home ranges, although there was a trend for turtles tracked with FastGPS tags to display larger homes ranges compared to turtles fitted with Arribada Horizon GPS tags (**Table S2.4**).

2.4.2. INTER-NESTING SITE FIDELITY

At least 2 complete theoretical inter-nesting intervals (i.e., 12 d duration each) were recorded for 45.45% of the tracked turtles (range: 2−6 inter-nesting intervals per individual). These turtles showed strong fidelity to inter-nesting sites over 2 randomly selected inter-nesting intervals (**Table S2.5**). Nevertheless, inter-individual variability was noticed with 77.44 ± 15.34% and 75.01 ± 18.58% of overlap between first and later inter-nesting intervals for 50 and 95% KUDs, respectively (**Table S2.5**).

We visually depicted overlapping home ranges and core areas for 3 turtles (PTT182458, PTT182451 and PTT60887; **Fig. 2.3**) and present the detailed example of one of these turtles (PTT60887, with the longest recording duration; **Table 2.2**), for which the true inter-nesting intervals (i.e., with varying durations) were assessed relying on direct observations from the beach patrols and on the fine-scale analysis of tracking data. The 50 and 95% KUDs of the 3 to 5 inter-nesting intervals recorded for the 3 individuals had a similar extent and a high overlap (**Table 2.2**, **Fig. 2.3**).

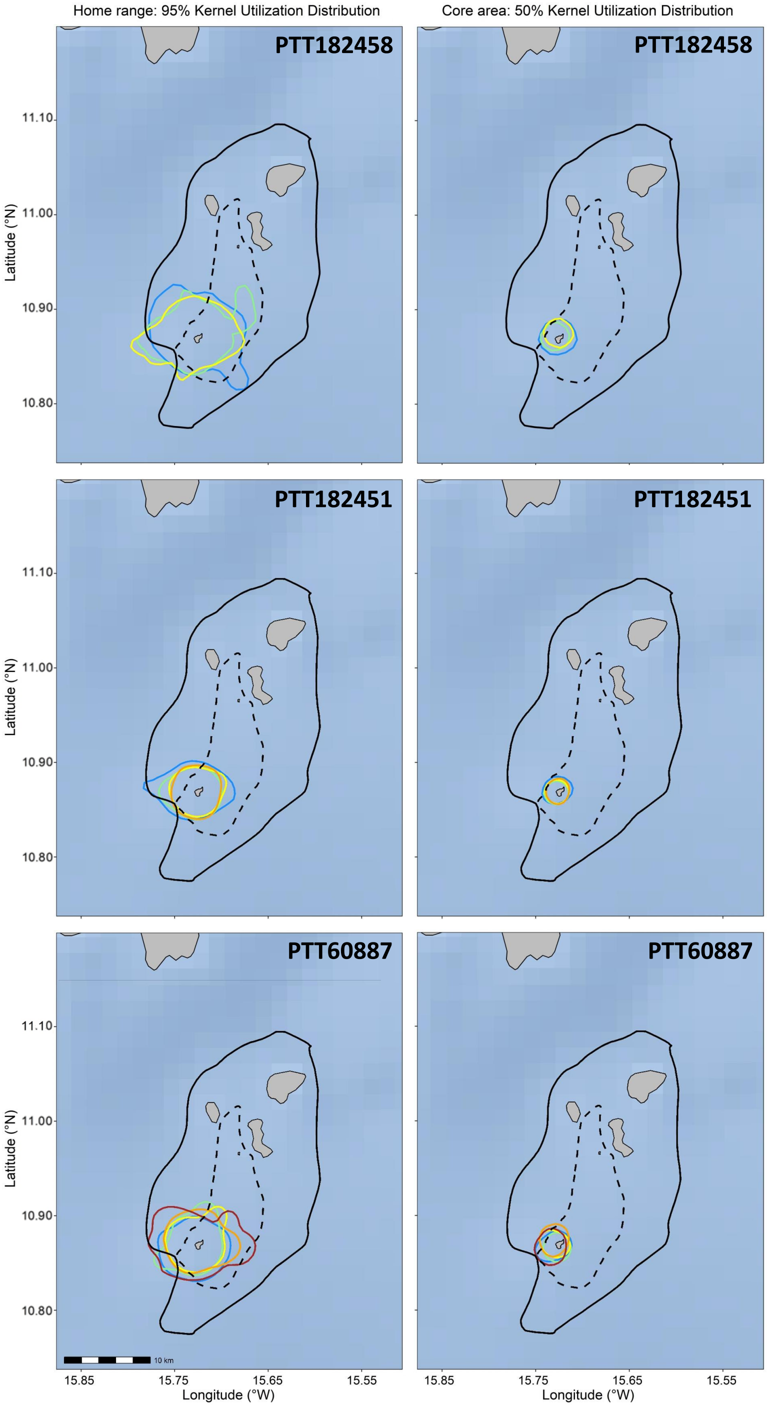

Fig. 2.3. Home ranges and core areas estimated over successive inter-nesting intervals for 3 female green turtles tracked within the Bijagós Archipelago, Guinea-Bissau. The dotted and solid black lines represent the contours of the no-take zone and the João Vieira-Poilão Marine National Park, respectively. Blue line: first recorded inter-nesting interval; green: second; yellow: third; orange: fourth; brown: fifth. The number of inter-nesting intervals differs among individuals

Table 2.2. Haul-out events (crawling/egg-laying) of a female green turtle (PTT60887). Most inter-nesting (IN) intervals were clearly identified through direct observations at the nesting beaches. Unobserved nesting attempts were estimated from tracking data if locations occurred ashore or very close to shore between dusk and dawn around the expected nesting date (i.e., corresponding to the date of the previous haul-out event plus the theoretical duration of the IN interval for this population, range: 8-17 d; Catry et al. 2009). Missing data are denoted by '–'

End date of IN intervals	Assessment of haul-out events	IN interval identifier	IN interval duration (d)	50% KUD (km²)	95% KUD (km²)	Overlap with 1st recorded IN interval (%)		Overlap with previous IN interval (%)	
						50% KUD	95% KUD	50% KUD	95% KUD
14/09/2018	Sat tag deployment date, laid eggs	–	–	–	–	–	–	–	–
29/09/2018	Estimated from tracking	1	14	11.54	48.69	–	–	–	–
06/10/2018	Encountered by the beach patrol, laid eggs	2	7	8.68	45.73	93.38	82.99	93.38	82.99
13/10/2018	Estimated from tracking	3	7	8.84	40.70	92.15	86.75	80.52	89.47
27/10/2018	Encountered by the beach patrol but not known if it laid eggs as it was found stranded on the rocks	4	14	10.16	48.99	74.09	79.93	77.04	77.76
06/11/2018	Encountered by the beach patrol, laid eggs	5	10	12.39	77.10	81.06	62.37	63.98	60.11

2.4.3. CONNECTIVITY BETWEEN NESTING SITES

Despite some tracked turtles performing incursions close to the islands of Meio and João Vieira (**Fig. 2.2A**), there was no clear evidence that they laid eggs in these or other nearby islands. The flipper tag observations from 2018 to 2020, on the other hand, revealed movements between the main nesting site of Poilão and the nesting areas of Meio and João Vieira. In 2018, 20 female turtles were flipper-tagged at Meio and resighted at Poilão (42.55% of 47 tagged turtles), while 1 female flipper-tagged at Poilão was resighted at Meio (0.35% of 288 tagged females in Poilão that year; **Table 2.3**). In 2020, 11 females that were flipper-tagged at Meio (13.10% of 84 tagged) were seen nesting at Poilão, and 1 turtle flipper-tagged at Meio was seen nesting at João Vieira (1.19%; **Table 2.3**).

Table 2.3. Evidence for connectivity between nesting beaches on the João Vieira-Poilão Marine National Park islands from female green turtles flipper-tagged during the 2018, 2019 and 2020 monitoring programs within the Bijagós Archipelago, Guinea-Bissau

Year	Location of observation	Location of re-observation	Number of re-observations	Total number of flipper-tagged females
2018	Meio	Poilão	20	47
2018	Poilão	Meio	1	288
2020	Meio	Poilão	11	84
2020	Meio	João Vieira	1	84

2.5. DISCUSSION

Understanding the spatial distribution of sea turtles during the breeding period is essential to the implementation of conservation measures or assessment of whether measures in place, such as MPAs, effectively support populations. We assessed the movement patterns of the largest breeding aggregation of green turtles in the Eastern Atlantic during inter-nesting intervals and the distribution of turtles according to the zonation of the JVPMNP. We found that females nesting on Poilão exhibited restricted movements around the island. They displayed strong fidelity towards their at-sea inter-nesting sites and limited connectivity to nearby islands within this MPA. The protection of this population during the breeding period can further be enhanced by increasing the no-take zone of the MPA.

2.5.1. INDIVIDUAL VARIATION IN HOME RANGES AND CORE AREAS

Female turtles tracked in this study mostly resided in overlapping and restricted inter-nesting habitats with similar extents and remained within shallow near-shore waters. Similar to our study, restricted inter-nesting areas have been previously reported among green (e.g., Chambault et al., 2016; K. M. Hart et al., 2017; K. M. Hart, Zawada, et al., 2013; Shimada et al., 2021), loggerhead *Caretta caretta* (e.g., Schofield, Hobson, Lilley, et al., 2010) and hawksbill (e.g., Hamilton et al., 2021; K. M. Hart et al., 2019; Revuelta et al., 2015; Walcott et al., 2012) turtles, although the use of larger areas has also been reported for green (e.g., Levy et al., 2017; Richardson et al., 2013), loggerhead (e.g., Levy et al., 2017; Snape et al., 2018; Tucker et al., 1995) and flatback *Natator depressus* (e.g., Hamann et al., 2017; Whittock et al., 2014, 2016) turtles.

Inter-individual variability exists, with larger turtles tending to display smaller core areas. It has previously been shown that smaller turtles tend to nest over larger ranges (Shimada et al., 2021), suggesting that inter-nesting ranges decrease with experience. Two turtles travelled longer distances north of the JVPMNP during the breeding period. These could potentially be newly recruited females, lacking knowledge of inter-nesting habitat availability and thus performing exploratory forays to evaluate alternative areas, or returning to known areas between clutches. These 2 animals were below the average size of nesting females from Poilão (100 cm CCL), supporting this hypothesis, as smaller individuals are presumably younger (Lockley et al., 2020; Şirin & Başkale, 2021). Notably, the smallest individual travelled twice to its foraging ground (approximately 50 km away from Poilão; Patrício et al., 2022) between consecutive nesting events.

Both core areas and home ranges of turtles were smaller when tag deployment occurred later in the breeding season. Hawksbill turtles have been shown to decrease their movements along the breeding season to save energy over consecutive inter-nesting intervals (Walcott et al., 2012). Green turtles may behave similarly at the JVPMNP.

2.5.2. EXTRINSIC FACTORS AFFECTING HOME RANGES AND CORE AREAS

The fact that longer recording durations led to larger home ranges and core areas was likely an effect of the number of recorded inter-nesting intervals and related proportion of locations recorded at the distal points of the trips. For instance, when testing for the tag type effect in 2019, turtles fitted with Arribada Horizon GPS tended to have smaller home ranges than those equipped with FastGPS. While Arribada GPS only recorded one inter-nesting interval per individual, FastGPS tags regularly recorded more than one inter-nesting interval, increasing the probability of larger KUDs.

A year effect was detected on the extent of the inter-nesting core areas and home ranges, with females having smaller core areas in 2019 than in 2018, and slightly larger home ranges in 2020 compared to 2018. Inter-annual variability in abundance was observed for nesting turtles at Poilão, with a lower number of nests estimated for 2019 compared to 2018 and 2020 (10,116, 14,406 and 59,676, respectively; IBAP, unpub. data). In years with high densities of nesting females, the expansion of inter-nesting core areas may decrease competition for preferred resting sites (L. D. Wood et al., 2017). Yet, the fact that we did not detect a year effect when comparing only 2019 (14,406 nests) with 2020 (59,676 nests) suggests that competition for resting sites is not noticeable in the waters surrounding Poilão Island, or perhaps the difference in abundance was not sufficient to lead turtles to explore larger areas to find suitable resting sites. Alternatively, the observed year effect may potentially be influenced by the use of the Argos system in 2018, which is less accurate and can lead to larger home ranges (Thomson et al., 2017). Further deployments using the same tag type across more years may elucidate this matter. Although the accuracy and number of locations as well as the recording duration are known to influence home range estimates (Börger et al., 2006; Dujon et al., 2014; Thomson et al., 2017), we are confident that the location system (Argos and/or GPS) had a negligible effect on the extent of the inter-nesting areas assessed from different tag types and on the assessments of overlap with the local MPA. Indeed, the proportion of GPS and Argos locations falling within the JVPMNP did not differ significantly (one-way ANOVA $F_{2,41} = 2.52$, $p = 0.09$; **Table S2.6**).

2.5.3. INTER-NESTING SITE FIDELITY

Tracked turtles for which at least 2 inter-nesting intervals were recorded exhibited strong fidelity to inter-nesting sites. This is consistent with studies conducted on green turtles in the Red Sea (Shimada et al., 2021) and at hawksbills nesting sites in Martinique (Nivière et al., 2018) and in Barbados (Walcott et al., 2012). Turtles probably return to the same inter-nesting areas where suitable conditions are found (K. M. Hart et al., 2010; Walcott et al., 2012), avoiding expending energy exploring unknown areas. Green turtles nesting at Poilão have also been shown to display high intra-season nest-site fidelity with 65.5% of clutches being laid within 150 m of the previous one from the same turtle (*n* = 110; Patrício et al., 2018). If most females return to nest in the same area of the beach, it might be a good strategy to stay within the same coastal inter-nesting area. Furthermore, by remaining near the nesting beaches, females can presumably save energy for oogenesis, trips to and from the nesting beach and egg-laying (Chambault et al., 2016; K. M. Hart et al., 2019; Walcott et al., 2012). Nonetheless, other satellite tracking (Esteban et al., 2015, 2017) and flipper tagging studies (Moncada et al., 2006) have shown that green turtles can shift their nesting sites over the course of the breeding period.

Inter-nesting area and nesting site selection among green turtles from Poilão Island can also be linked to benthic topography. We found that turtles nesting in beach sectors surrounded by a barrier of intertidal rocks tended to display smaller home ranges. Potentially, turtles crossing rocky areas to reach nesting sites may have prior knowledge of these formations, that they may use as resting sites, a behaviour known to occur among green and hawksbill turtles (Fernandes et al., 2017; Reisser et al., 2013; Walcott et al., 2014). In Brazil, a green turtle was found resting under the same rock twice (Reisser et al., 2013), suggesting that turtles can find known features, avoiding the energy costs of looking for new resting sites during each inter-nesting interval. Previous studies estimate that green turtles prefer resting depths of 10 to 20 m, where they reach neutral buoyancy (Hatase et al., 2006; Hays et al., 2000; I-Jiunn, 2009). Here, turtles used shallower depths (2.3 to 6.0 m) so assisted resting is probably the best option to save energy. Reconstructing the time-energy budget of inter-nesting females would, however, require the use of time-depth recorders (Ballorain et al., 2013; Hazel et al., 2009) and accelerometers (Hounslow et al., 2022).

2.5.4. CONNECTIVITY BETWEEN ISLANDS

Our tracking data did not clearly indicate connectivity between Poilão and the other islands of the JVPMNP during the breeding period. High nest-site fidelity towards Poilão beaches (Patrício et al., 2018) further supports overall restricted linkages between the nesting islands, despite their close proximity. However, connectivity between JVPMNP islands is supported by resightings of individuals flipper-tagged at Meio Island and later found nesting at Poilão. Connectivity between nesting sites has been reported in other nesting green and hawksbill turtle populations (Esteban et al., 2015; Hamilton et al., 2021; K. M. Hart, Zawada, et al., 2013; Iverson et al., 2016), a strategy that can yield evolutionary advantages and enhance overall reproductive success (Hamilton et al., 2021; K. M. Hart et al., 2019; Schofield, Hobson, Lilley, et al., 2010), particularly if nesting beaches are subjected to variable levels of threats (e.g., sea level rise, predation or poaching). We suggest reinforcing the beach monitoring on other islands besides Poilão to estimate the reproductive success and suitability of the MPA to enhance population resilience on each of the JVPMNP islands. Since a population may be overestimated if counts of turtles are performed independently on different islands (Esteban et al., 2017), detailed information on connectivity between islands is essential for conservation management of turtles within the JVPMNP.

2.5.5. ADEQUACY OF MPA LIMITS

We show that female green turtles spent most of the peak breeding season within the limits of the JVPMNP. These findings reinforce the value of MPAs around important sea turtle rookeries. Similar findings have been described for the Solomon Islands (Hamilton et al., 2021), Dominican Republic (Revuelta et al., 2015) and the Chagos Archipelago (Hays, Mortimer, et al., 2014).

However, we further reveal that only 52% of the overall home range of tracked turtles fell within the central no-take zone of this MPA. We assume that the population spends half of its inter-nesting time within the peripheral zone of the JVPMNP, where turtles coexist with anthropogenic activities including recreational and artisanal fishing. Extending the no-take zone to encompass the area westwards of Poilão would reduce overlap between fishing activities and the habitat of turtles during the critical breeding period, enhancing the protection of turtles. This extension could be temporally restricted (A. J. B. Santos et al., 2021; Schofield et al., 2013; A. C. C. D. Silva et al., 2010; Witt et al., 2008) to the peak nesting season (August to September) if the fishing grounds immediately west of Poilão are very important for local fishers, to reduce conflict.

Additionally, despite restrictions in place, illegal fishing still occurs inside this MPA (C. Barbosa, pers. comm.), perpetrated by national (38%) and foreign (62%) fishers (Catry et al., 2018), leading to turtle bycatch. We thus recommend increasing the frequency of at-sea patrolling within the waters of the park and enforcing existing regulations, particularly during the green turtle peak breeding season. Protection measures directed at female turtles will also benefit the reproductive males as a recent study shows that most males concentrate near Poilão Island during the peak breeding season (Beal et al., 2022). The risk of interaction between turtles and fishing activities outside of the peak breeding season is probably low, as both females (*n* = 35) and males (*n* = 12) migrate to foraging areas outside the JVPMNP (Beal et al., 2022; Patrício et al., 2022), suggesting that these coastal waters are not used for foraging.

CHAPTER 3

INTER-ISLAND NESTING DYNAMICS AND CLUTCH SURVIVAL

INTER-ISLAND NESTING DYNAMICS AND CLUTCH SURVIVAL OF GREEN TURTLES *CHELONIA MYDAS* WITHIN A MARINE PROTECTED AREA IN THE BIJAGÓS ARCHIPELAGO, WEST AFRICA

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Published: (2024). Inter-island nesting dynamics and clutch survival of green turtles *Chelonia mydas* within a marine protected area in the Bijagós Archipelago, West Africa. *Marine Biology*, 171, 143. https://doi.org/10.1007/s00227-024-04463-w

3.1. ABSTRACT

Understanding spatial heterogeneity in reproductive success among at-risk populations facing localised threats is key for conservation. Sea turtle populations often concentrate at one nesting site, diverting conservation efforts from adjacent smaller rookeries. Poilão Island, Bijagós Archipelago, Guinea-Bissau, is a notable rookery for green turtles *Chelonia mydas* within the João Vieira-Poilão Marine National Park, surrounded by 3 islands (Cavalos, Meio and João Vieira), with lower nesting activity. Poilão's nesting suitability may decrease due to turtle population growth and sea level rise, exacerbating already high nest density. As the potential usage of secondary sites may arise, we assessed green turtle clutch survival and related threats in Poilão and its neighbouring islands. High nest density on Poilão leads to high clutch destruction by later turtles, resulting in surplus eggs on the beach surface and consequently low clutch predation (4.0%, *n* = 69, 2000). Here, the overall mean hatching success estimated was 67.9 ± 36.7% (*n* = 631, 2015–2022), contrasting with a significantly lower value on Meio in 2019 (11.9 ± 23.6%, *n* = 21), where clutch predation was high (83.7%, *n* = 98). Moderate to high clutch predation was also observed on Cavalos (36.0%, *n* = 64) and João Vieira (76.0%, *n* = 175). Cavalos and Meio likely face higher clutch flooding compared to Poilão. These findings, alongside observations of turtle exchanges between islands, may suggest a source-sink dynamic, where low reproductive output sink habitats (neighbouring islands) are utilized by migrants from Poilão (source), which currently offers the best conditions for clutch survival.

3.2. INTRODUCTION

Understanding the spatial heterogeneity of reproductive success among populations of conservation concern is critical to develop and implement effective measures for their safeguarding and guide the allocation of conservation efforts (Assersohn et al., 2021; Hays et al., 2019; Welbergen et al., 2020). This is particularly important for populations facing localised threats (Allen & Singh, 2016), as dispersing breeding efforts may counteract the effect of restricted reproductive failures (e.g., Bowen et al., 1989; Refsnider & Janzen, 2010). Occasionally, locally threatened populations may exhibit source-sink dynamics, where sink habitats (those where reproductive success is low) are persistently used, sustained by nearby abundant sources of reproductive individuals (Pulliam, 1988; Pulliam & Danielson, 1991). The potential for these sink habitats to confer protection can change in the medium and long term, particularly under global environmental changes.

Sea turtles, a group of conservation concern (Godley et al., 2020) that depends on sandy beaches for egg incubation, often aggregate at one geographically restricted nesting site, with this site being the target of long-term conservation efforts. This can result from the geographic isolation of nesting sites, as in the case of the green turtle *Chelonia mydas* rookeries at Ascension (Mortimer & Carr, 1987) and Raine Islands (Hamann et al., 2022). But even when other seemingly suitable nearby nesting habitats exist, populations may largely concentrate at specific sites (for instance, approximately 75% of the loggerhead turtle *Caretta caretta* nesting in the entire Cabo Verde Archipelago concentrate in Boa Vista Island; Marco et al., 2012, 2015). The underlying causes for this can be varied and multifactorial, and may be linked to historical preservation of turtle nesting sites associated with cultural traditions (Liu, 2017), limited human access or low human population density (Catry et al., 2002), distinct local environmental conditions and philopatric behaviour (Stiebens et al., 2013).

Since sea turtles offer no parental care, nest-site selection is fundamental for offspring survival (Patrício et al., 2018). During incubation, the developing embryos can be exposed to harmful environmental conditions, such as extreme high sand temperatures or flooding (Booth, 2017; Fuentes & Cinner, 2010; Limpus et al., 2020; Maurer et al., 2021; Montero et al., 2018; Pike, 2014). On several beaches, predation is also a major source of embryo and hatchling mortality (Z. P. Butler et al., 2020). Predator species vary geographically, and may include mammals, birds, reptiles and crabs (H. J. Stokes et al., 2024). Several studies suggest that nesting turtles may rely on environmental cues to choose nesting sites (D. S. Wilson, 1998; D. W. Wood & Bjorndal, 2000), and may even select beaches with reduced predatory activity (R. Martins et al., 2022), enhancing clutch survival.

Sea turtles are however generally limited in their nest-site choice, as they display natal homing, returning to the geographic area where they hatched to reproduce (Brothers & Lohmann, 2015; Levasseur et al., 2019; Lohmann & Lohmann, 2019). Additionally, some species exhibit high nest-site fidelity, laying consecutive clutches on the same beach (Heredero Saura et al., 2022; Kamel & Mrosovsky, 2004), within the same location of the beach (Kamel & Mrosovsky, 2005, 2006; Patrício et al., 2018; Shimada et al., 2021), even across nesting seasons (Heredero Saura et al., 2022). However, limited nest-site plasticity has also been reported for different sea turtle populations (Esteban et al., 2015, 2017; Hamilton et al., 2021; K. M. Hart, Zawada, et al., 2013; Iverson et al., 2016). This plasticity can strengthen overall reproductive success (Hamilton et al., 2021; K. M. Hart et al., 2019; Schofield, Hobson, Lilley, et al., 2010) and increase the ability to cope with the loss or degradation of nesting areas (Esteban et al., 2017), for example through the colonisation of new areas (Luna-Ortiz et al., 2024).

The Bijagós Archipelago, in Guinea-Bissau, West Africa, gathers one of the largest breeding aggregations of green turtles globally (Patrício et al., 2019) and thus is a key area for the conservation of this species. Nesting occurs on several islands of the Bijagós, but the vast majority of clutches are laid on Poilão, a small island located in the southeast of the archipelago, within a marine protected area (MPA), the João Vieira-Poilão Marine National Park (hereafter ‘JVPMNP’; Catry et al., 2009). The mean number of clutches per year at Poilão was estimated at ca. 25,000 from 2017 to 2021 (Catry et al., 2023), and the number of nests per year has been increasing in the last 20 years (A. Broderick & Patrício, 2019; Patrício et al., 2019; IBAP, unpub. data). Besides Poilão, this MPA encompasses 3 other islands where sea turtles also nest (Catry et al., 2002, 2009). However, the nesting population is highly concentrated on Poilão. This island is expected to face increased vulnerability to climate change-related threats in the near future, including rising incubation temperatures and expanding flooded areas due to sea level rise (SLR; Patrício et al., 2019). Furthermore, the high nest density at Poilão can potentially result in density-dependent nest destruction by later nesting turtles (Booth et al., 2020) and enhance the spread of pathogens, reducing clutch survival (Bézy et al., 2015).

As Poilão may become less suitable for nesting due to population growth and climate change, it is important to explore the potential of neighbouring islands as alternative rookeries. Here, we aim to assess clutch survival and associated threats at Poilão and at the 3 nearby islands within the JVPMNP. To do this, we (i) estimate the total number of nests and (ii) quantify clutch predation and nest flooding events within the JVPMNP. Additionally, we estimate the hatching success at Poilão and one of its neighbouring islands for which data is available.

3.3. MATERIALS AND METHODS

3.3.1. STUDY SITE

The João Vieira-Poilão Marine National Park (JVPMNP) is located on the southeast of the Bijagós Archipelago, in Guinea-Bissau, West Africa (N11°17’, W15°58’; **Fig. 3.1A**). The park encompasses a total area of 49,500 ha, of which approximately 1,485 ha corresponds to the 4 main islands (Poilão, Cavalos, Meio and João Vieira), all fringed by low-lying sandy beaches. The 43 ha island of Poilão (10°52’N, 15°43’W; **Fig. 3.1B**) is the smallest and hosts the largest green turtle rookery in the archipelago (Catry et al., 2002, 2009) and the second largest in the Atlantic (A. Broderick & Patrício, 2019). João Vieira (11°02’N, 15°38’W; **Fig. 3.1B**), Meio (10°58’N, 15°40’W; **Fig. 3.1B**) and Cavalos (11°00’N, 15°42’W; **Fig. 3.1B**) have areas of 900, 402 and 210 ha, respectively. The main green turtle breeding season at the JVPMNP extends from mid-June to mid-December, with a peak nesting activity in August and September (Catry et al., 2002).

Poilão is considered a sacred site to local communities and human presence is forbidden except for rare traditional events and sea turtle monitoring activities, which enhances effective turtle protection (Barbosa, Pires, et al., 2018; Catry et al., 2009). Of the 3 remaining islands, João Vieira is the only one with permanent human occupation, consisting of very few people running a seasonal touristic facility. However, João Vieira and Meio annually host seasonal fishing camps and, from time to time, farmers and their families settle on these islands to engage in slash-and-burn rice agriculture, locally known as “m’pam-pam” (Barbosa, Pires, et al., 2018; Catry et al., 2018). These families, primarily from Canhabaque Island but also from other islands within the archipelago, reside there for several months until the harvesting period. Historical records indicate that the slash-and-burn rice agriculture was performed in João Vieira in 2002, 2006 and 2017, and in Meio in 1986, 2009, 2012 and 2014 (Catry et al., 2018). The practice of slash-and-burn rice agriculture near the beach can reduce the availability of shaded, cooler nesting sites for sea turtles (Patrício et al., 2017), thus decreasing male hatchling production and potentially decreasing the availability of sites with optimal thermal conditions for egg incubation under future global warming (Patrício et al., 2017). Additionally, this agricultural practice is associated with the consumption of turtle meat (Barbosa, Patrício, et al., 2018). In the last harvesting period at Meio in 2014, a minimum of 87 adult female turtles were reported to be poached, although the actual number of turtles killed and consumed may have been significantly higher (Barbosa, Patrício, et al., 2018). Similarly, the camping of seasonal fishers may contribute to the use of females as a food source, thereby increasing mortality rates. Cavalos is not sought for these practices and human influence resumes to the presence of feral pigs, a known sea turtle nest predator (Cruz et al., 2005; Hitipeuw et al., 2007; Whytlaw et al., 2013; Zárate et al., 2013).

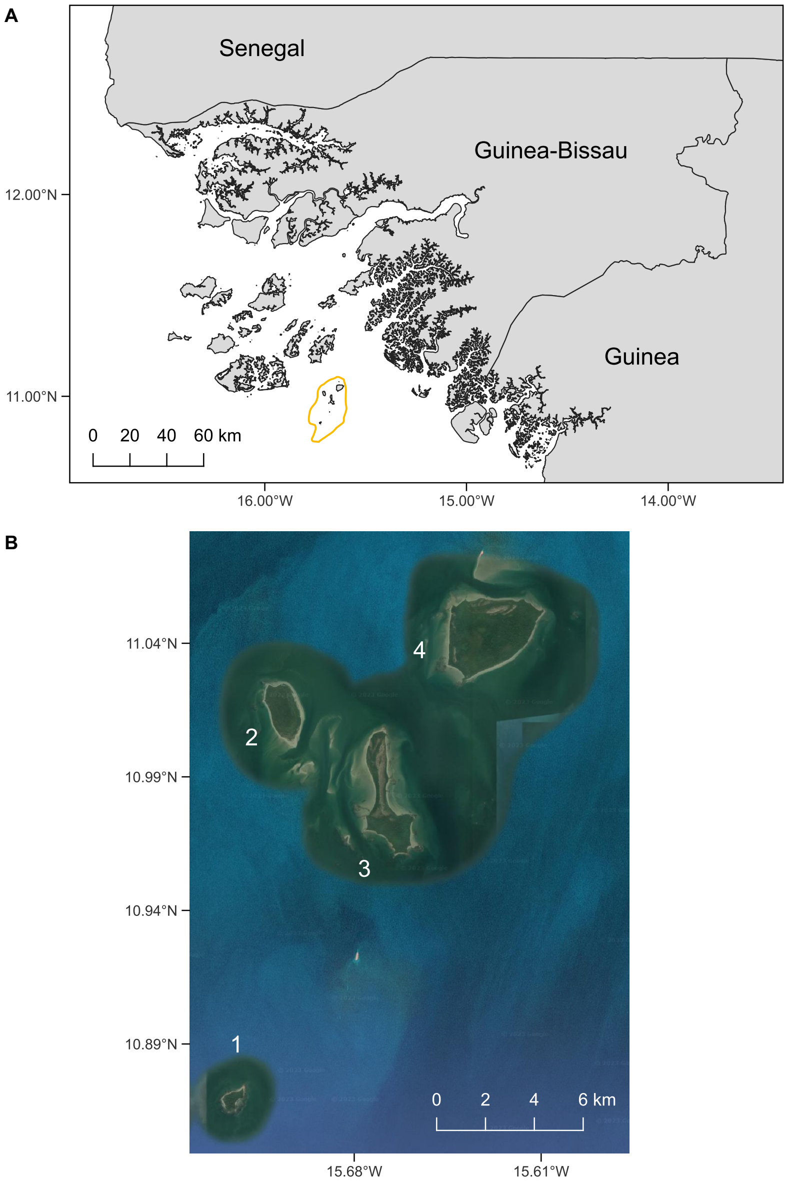

Fig. 3.1. (A) Location of the study sites (yellow): João Vieira-Poilão Marine National Park (JVPMNP), Bijagós Archipelago, Guinea-Bissau. **(B)** Islands of the JVPMNP: (1) Poilão, (2) Cavalos, (3) Meio and (4) João Vieira. The yellow line depicts the limits of the JVPMNP

3.3.2. RELATIVE NESTING ABUNDANCE PER ISLAND

Green turtle nesting activity has been continuously monitored at Poilão throughout most of the breeding season (from August to November) since the year 2000, by the Instituto da Biodiversidade e das Áreas Protegidas (in english Institute of Biodiversity and Protected Areas, IBAP) of Guinea-Bissau (Barbosa, Patrício, et al., 2018), and since 2007 monitoring protocols were standardized. Each night, the IBAP patrols the beach around the peak of the high tide (see Patrício et al., 2018) to count all females encountered on the beach, and each morning (between 06:00 and 08:00) the number of turtle tracks from the previous night are recorded. Monitoring of nesting activities (daily and nightly surveys) at Meio started in 2019, but only from August to October. This shorter monitoring period precludes systematic nest exhumation since a large proportion of clutches have yet to hatch by the end of the monitoring campaign. At João Vieira, the monitoring began in 2020, with daytime beach surveys conducted twice a week, usually between August and October. No regular monitoring is conducted at Cavalos. The differences in monitoring levels across the 4 islands of the park result from the difficulty and high costs to access these remote sites. For this study, we used the green turtle nesting database from Poilão, along with all available nesting data from Meio (2019, 2020 and 2021), João Vieira (2011, 2020 and 2021) and Cavalos (2016).

To estimate the total number of nests laid by breeding turtles at Poilão, we relied on the counts of turtle tracks. This approach is necessary due to the high nest density at Poilão, which makes it impractical to accurately count all nests, as the activity of new turtles obscures the tracks left by earlier ones. Consequently, we first used linear interpolation, based on the number of tracks noted in the previous and following days, to estimate the number of tracks on rare occasions when weather conditions precluded beach surveys (Godley et al., 2001). Then, we divided the resulting total number of tracks by 2 (ascending and descending tracks) to obtain the number of nesting female emergences, and multiplied this figure by 0.813, to adjust for nesting success in Poilão estimated by Catry et al. (2009) (81.3%, $n = 75$ monitored adult female emergences). The temporal distribution of nesting is well known at Poilão from earlier census, and thus, to account for a short period at the onset and at the end of the breeding season when no track counts were performed, we multiplied the previous estimate (i.e., tracks/2 x 0.813) by a factor of 1.05, following Catry et al. (2009).

For the other islands, the actual number of nests were counted during surveys. We assumed that the green turtle temporal nesting distribution was consistent across islands. This decision was based on local observations confirming synchronous nesting patterns across the JVPMNP. Hence, we used the known temporal distribution of green turtle nesting at Poilão as a model to extrapolate the number of nests observed during surveys at Cavalos, Meio and João Vieira to the entire breeding season.

3.3.3. TURTLE NEST DENSITIES PER ISLAND

We estimated the available nesting areas at Cavalos, Meio and João Vieira by using Google Satellite Imagery in QGIS version 3.26 software. On the high-resolution images of the islands, we delimited the available nesting area per island using the QGIS Create Layer tool, and then calculated the area of the polygons using the $area function. We considered ‘available nesting area’ as the sandy areas above the high tide line. This is a very broad approximation since some areas may be perceived as suitable in the satellite images but be regularly flooded, while some areas under the forest border canopy were not detectable using satellite imaging. For Poilão, we used the estimation of the available nesting area previously published (Patrício et al., 2018), which was based on on-site measurements. The spatial density of green turtle nests was calculated by dividing the number of estimated nests by the estimated available nesting area, for each survey year.

3.3.4. HATCHING SUCCESS AT POILÃO AND MEIO

To assess green turtle hatching success at Poilão, up to 4 nests per night were uniquely numbered and marked with wooden sticks, between August and October, from 2013 to 2022, and surveyed daily until nest excavation (1−5 d after hatchling emergence). Because in 2013 and 2014 the clutches were given extra protection using larger, reinforced wooden sticks, which may have prevented disturbances such as destruction by other turtles, we discarded these 2 years from the hatching success estimations. Upon nest exhumations, after hatchling emergence, we recorded the number of hatched and unhatched eggs, and of live and dead hatchlings found inside the nest chamber. Then, we estimated clutch size (the sum of hatched and unhatched eggs) and hatching success (number of hatched eggshells / clutch size). On occasions, the whole clutch was washed by spring tides, and we considered hatching success to be zero. Additionally, some nests were ‘lost’ due to the displacement or covering with sand of wooden sticks by turtles. It is important to note that the term ‘lost’ does not necessarily imply complete loss or a hatching success rate of zero. Some of the ‘lost clutches’ were likely partially or totally destroyed by the action of nesting turtles while digging the body pit, the egg chamber or while covering their nest. However, many others probably remained intact, raising the possibility that ‘lost clutches’ may have had higher hatching success rates (>0%). The fate of these ‘lost clutches’ remains uncertain, and as we cannot determine the extent of potential success (ranging from 0 to 100%), we initially discarded them from the estimation of hatching success. Acknowledging the potential for overestimation of hatching success resulting from this approach, we also calculated the mean annual hatching success rates attributing a hatching success value of zero to all ‘lost clutches’.

We used a Kruskal-Wallis test to compare hatching success across years. We then calculated the non-parametric Spearman’s rank correlation coefficient to test the association between the mean hatching success and the number of estimated nests per breeding season. In 2019, hatching success was estimated at Meio for a subset of 21 clutches laid between

August 3 and August 28, which were monitored until hatching. The hatching success formula used for Meio was the same as that used in Poilão. Hatching success was not estimated at Cavalos or João Vieira for any of the study years due to the absence of teams in the field during the hatching season.

3.3.5. CLUTCH PREDATION AND FLOODING

Clutch predation at Poilão was previously published in Catry et al. (2002). An accurate monitoring of the number of nests that were at least once covered by the tide or flooded by rainfall exists only for the years 2013 and 2014.

In the remaining islands, dedicated surveys were conducted to estimate the levels of clutch predation and flooding, specifically in 2011 at João Vieira (only clutch predation was recorded), in 2016 at Cavalos, and in 2019 at Meio. During these surveys, nests were marked with wooden sticks and monitored during the first 10 d after oviposition, since this is the period of peak predatory activity (Barbosa, Patrício, et al., 2018; Leighton et al., 2011). Clutch predation by Nile monitors *Varanus niloticus* and ghost crabs *Ocypode cursor* (the most common egg predators in the park; Barbosa, Patrício, et al., 2018) was identified by the presence of fresh eggshells scattered around the nests, along with these species' distinctive tracks. Confirmation was obtained in a number of nests located in João Vieira Island by the use of time-lapse cameras. We defined the occurrence of a flooding event as the submersion of a nest in water, resulting from high tide or rainfall.

3.4. RESULTS

3.4.1. RELATIVE NESTING ABUNDANCE AND DENSITY PER ISLAND

There was a high inter-annual variation in the abundance of green turtle nests in Poilão from 2007 to 2022. The number of estimated nests per breeding season fluctuated between a minimum of 4,176 in 2012 and a maximum of 71,032 in the peak year of 2020, with an average (± SD) of 32,608 ± 33,327 nests per year in the interval 2020−2022 (*n* = 97,824 estimated nests between 2020 and 2022). Poilão hosts approximately 90% of the nests within the JVPMNP (**Table 3.1**).

The number of estimated nests per year on the islands of Cavalos, Meio and João Vieira ranged from 38 to 2,461 (**Table 3.1**). These correspond to 0.2% (on João Vieira in 2021) to 7.7% (on Cavalos in 2016) of the nests at Poilão in the same years (**Table 3.1**). Cavalos is the island hosting more nests after Poilão, followed by Meio and then João Vieira. On the 2 islands for which there are estimates of the number of nests for the 2 most recent years (Meio and João Vieira), these follow the inter-annual variation of the nesting abundance in Poilão (**Table 3.1**). However, the percentage of nests in João Vieira in relation to Poilão decreased from the earlier survey in 2011 in comparison to the 2 most recent surveys (**Table 3.1**). Across all survey years, nest densities at Cavalos, Meio and João Vieira were much lower than those estimated for Poilão, ranging from 0.002 to 0.206 nests m^{-2} (**Table 3.1**). In comparison, for the same survey years, nest densities at Poilão were consistently one order of magnitude higher, varying between 0.44 and 2.04 nests m^{-2} (**Table 3.1**).

3.4.2. HATCHING SUCCESS AT POILÃO AND MEIO

The estimated mean (± SD) hatching success for green turtles at Poilão between 2015 and 2022 was 67.9 ± 36.7% (*n* = 631 monitored nests until hatching, ranging between 42.5 ± 39.1% in 2020, *n* = 72 monitored nests, and 84.4 ± 22.9% in 2016, *n* = 55 monitored nests). Hatching success at Meio in 2019 was low: 11.9 ± 23.6% (mean ± SD, *n* = 21 monitored nests until hatching). Unsuccessful nests had signs of predation by Nile monitors and ghost crabs.

At Poilão, hatching success varied significantly across years (Kruskal-Wallis test, H_7 = 93.367, $p < 0.001$; **Fig. 3.2**). There was no relation between the mean hatching success and the number of estimated nests per breeding season (Spearman rank correlation, rs = -0.40, *n* = 8, *p* = 0.32; **Fig. S3.1**). Between 2015 and 2022, the location of 222 out of the 853 (26.0%) monitored nests was lost. Given the possibility of an overestimation of the hatching success (by excluding lost clutches from the analysis), we recalculated this parameter attributing a hatching success value of zero to all monitored nests for which we lost their location. We emphasize that this approach underestimates the actual hatching success by assuming that all ‘lost clutches’ had 100% mortality. Under this assumption, overall mean (± SD) hatching success was 49.7 ± 43.5% (*n* = 853 monitored nests; **Fig. S3.2**), and varied across years (**Fig. S3.2**), with significant lower mean (± SD) hatching success in 2020 (26.4 ± 37.1%, *n* = 116 monitored nests; **Fig. S3.2**), but still much higher than the single estimate for Meio.

3.4.3. CLUTCH PREDATION AND FLOODING

Predation was highly variable across the JVPMNP, being very low at Poilão and moderate to very high at the remaining islands (**Table 3.2**). The Nile monitor was the main nest predator on all islands (**Table 3.2**). Out of the 175 monitored nests for predation at João Vieira, 22 (12.6%) were simultaneously observed using time-lapse cameras. The video footage confirmed that Nile monitors were the exclusive species preying on green turtle nests here, accounting for 100% of the observed instances (*n* = 74).

Table 3.1. Number of green turtle nests (counted and estimated) on the islands of Cavalos, Meio and João Vieira, located in the João Vieira-Poilão Marine National Park, Bijagós Archipelago, Guinea-Bissau, in the years studied. Percentage of nests in each of these islands compared to the main nesting site of Poilão in the same year. Estimated nest densities for each island of the park

Nesting site	Year	Surveyed period	Days of survey (d)	Number of nests during the surveyed period	Estimated number of nests for the breeding season	Estimated number of nests at Poilão in the same year	Percentage of nests compared to Poilão in the same year	Estimated nest densities (nests m^{-2})	Estimated nest densities at Poilão in the same years (nests m^{-2})
Cavalos	2016	06/08/2016–08/09/2016	34	852	2,461	31,892	7.7	0.038	0.92
Meio	2019	03/08/2019–11/10/2019	70	191	266	10,685	2.5	0.027	0.31
	2020	09/08/2020–29/10/2020	82	1609	2,017	71,032	2.8	0.206	2.04
	2021	08/08/2021–29/10/2021	83	323	401	15,232	2.6	0.041	0.44
João Vieira	2011	06/09/2011–30/09/2011	25	596	2,028	34,111	5.9	0.085	0.98
	2020	11/08/2020–19/09/2020	40	205	446	71,032	0.6	0.019	2.04
	2021	08/08/2021–31/10/2021	85	31	38	15,232	0.2	0.002	0.44

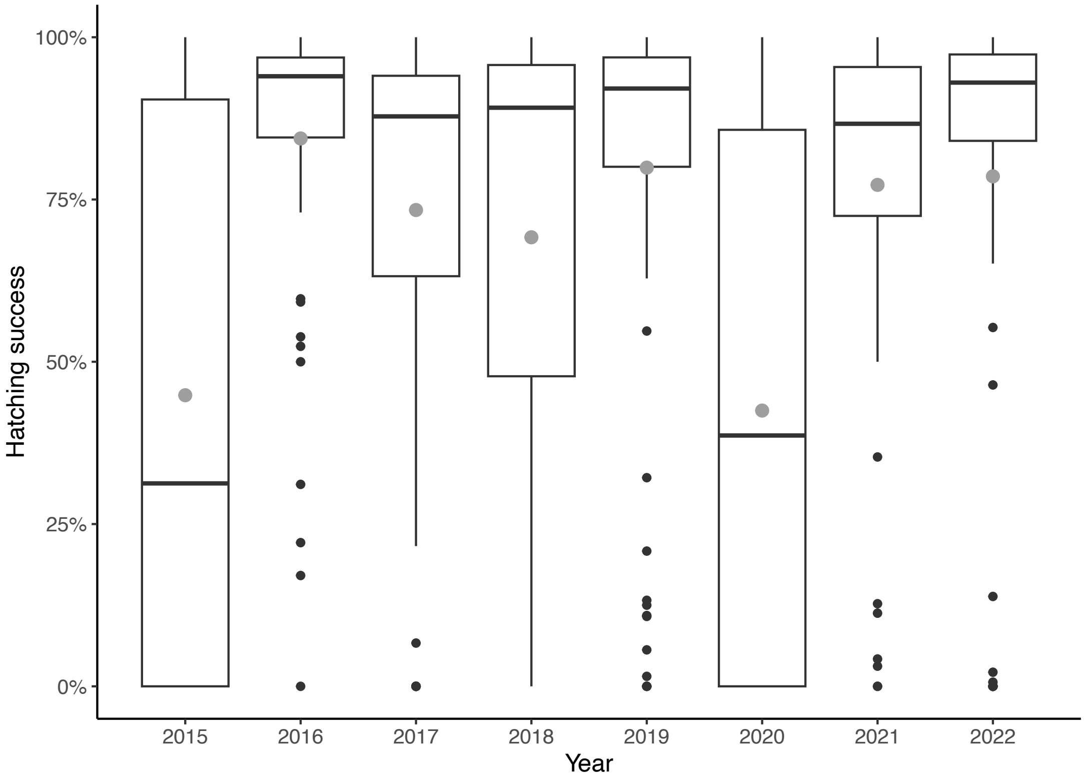

Fig. 3.2. Green turtle hatching success (excluding all lost clutches from the calculation) between 2015 and 2022 on Poilão, Bijagós Archipelago, Guinea-Bissau. Boxplots include the median, 25th and 75th percentiles and outliers. The mean hatching success for each year is illustrated by the grey dots

Flooding incidence differed among islands, affecting less than 25% of the nests at Poilão, to over 40% at Cavalos (**Table 3.2**). At Poilão, where nest exhumations were conducted, we were able to determine the hatching success of flooded clutches. Here we used the data from 2013 and 2014, when large, reinforced wooden sticks were used to prevent clutch destruction by other turtles (as mentioned above), to specifically evaluate the impact of flooding.

In 2013, the mean (± SD) hatching success for flooded nests at Poilão was 48.4 ± 41.2% (*n* = 58 monitored nests), with 38.5% of these clutches having 0.0 to 4.2% hatching, and the remaining with values between 50.0 and 97.9%. In 2014, mean (± SD) hatching success of flooded nests at Poilão was 35.7 ± 26.4% (*n* = 66 monitored nests). Among these, one clutch was entirely unsuccessful, whereas the remaining 98.5% had hatching rates varying from 25.0 to 91.5%. We have no data on nest flooding for the island of João Vieira.

Table 3.2. Proportion of green turtle clutches that were lost to predation and flooding on the João Vieira-Poilão Marine National Park islands, Bijagós Archipelago, Guinea-Bissau. Predators of green turtle nests are also identified. Missing data are denoted by '–'

Nesting site	Year	Number of monitored nests	Predated clutches (%)	Predators	Flooded clutches (%)
Poilão	2000	69	4.0	Nile monitors (3.0%) Ghost crabs (1.0%)	24.0 (2013) 12.0 (2014)
João Vieira	2011	175	76.0	Nile monitors (100.0%)	–
Cavalos	2016	64	36.0	Nile monitors (30.0%) Ghost crabs (6.0%)	42.0
Meio	2019	98	83.7	Nile monitors (75.5%) Ghost crabs and Nile monitors (7.1%)	36.7

3.5. DISCUSSION

Our study compiles information from 4 islands within the João Vieira-Poilão Marine National Park (JVPMNP) in Guinea-Bissau, including the important green turtle rookery at Poilão, to assess reproductive output parameters and evaluate habitat suitability across these diverse sites. We show that the prevalence of clutch predation and/or flooding was higher on the satellite rookeries. Lower survival at satellite colonies and the maintenance of linkages between islands may suggest the existence of a source-sink dynamic.

3.5.1. HATCHING SUCCESS

The mean hatching success found in this study (67.9 ± 36.7%, excluding all lost clutches from the calculation), is close to what was previously reported (2013−2014: 65.4 ± 33.9%; Patrício et al., 2017), and within the range of values described for other green turtle rookeries, e.g., on Ascension Island (57.0−85.0%; A. C. Broderick et al., 2001) and on Akyatan Beach, Turkey (58.0−67.0%; Turkozan et al., 2011). Nevertheless, both higher (91.6%, Akumal, Quintana Roo, Mexico; K. C. Santos et al., 2017) and lower (42.0−57.0%, Tortuguero, Costa Rica; Fowler, 1979; 46.0%, Galápagos Islands; Zárate et al., 2013) values of mean hatching success have also been reported. Assuming 100% mortality for all nests with lost locations probably resulted in an underestimate of the hatching success, given that lost nests likely include a mix of disturbed and undisturbed clutches. Nonetheless, this exercise shows that even under the most conservative estimate, Poilão nesting grounds still guarantee mean to high hatching success on several years (3 out of 8 years with hatching success above 50%; **Fig. S3.2**). It is important to emphasize that our estimation of clutch size involved counting both hatched and unhatched eggs during nest exhumations. Previous research has shown that at sites where nest predation by crabs is prevalent, there may be a tendency for clutch size to be underestimated (H. J. Stokes et al., 2024). However, in the case of Poilão, while we acknowledge the occurrence of nest predation, it typically occurs at low intensity (Catry et al., 2002). Therefore, given the limited impact of nest predation in Poilão, the likelihood of bias in our clutch size estimates is low.

Generally, a higher number of nests on Poilão did not correspond to a decrease of average hatching success rates. This suggests that, on most years, turtles are not yet overcrowding the available nesting space. In 2020, however, the low hatching success observed may have been a density-dependent phenomenon, wherein an exceptionally large number of nesting turtles resulted in increased clutch disturbance. In this peak nesting year, under the assumption of uniform nest distribution throughout the beach, our estimations suggest a density of over 2 nests per square meter at Poilão. We know however that some sections of the beach are more heavily used (Patrício et al., 2018), and in these preferred areas the nest density can be considerably higher, potentially reaching a level that affects clutch survival, for example, through increased clutch disturbance or reduced available oxygen.

3.5.2. CLUTCH SURVIVAL AND MORTALITY FACTORS

Whilst Poilão exhibits a high concentration of green turtle nests, nest predation is very low. This may result from a density-dependent predator satiation effect (Eckrich & Owens, 1995). At Poilão, nesting turtles destroy a high number of clutches (Catry et al., 2009), therefore, there is a considerable amount of aboveground scattered eggs available to consumers, and predators do not need to excavate nests actively searching for this food source. Despite nest destruction also contributing to mortality, hatching success at Poilão consistently maintained mean to high levels over several years, even with the assumption that all lost clutches were entirely destroyed. In contrast, predation significantly reduces hatching success on Meio, the other island for which we were able to estimate hatching success. However, it should be noted that the low sample size used for hatching success estimation and the lack of inter-annual data available for Meio are 2 limitations of this study. Overall, predation on other islands of the JVPMNP impacted a moderate to very high proportion of green turtle clutches. Several studies have reported similar values of nest predation to those found in our study (e.g., 27.7%; Engeman et al., 2003; 44.9%; Z. P. Butler et al., 2020; 53.3%;

Engeman et al., 2005; 89.6%; Whytlaw et al., 2013). Within the Bijagós Archipelago, sea turtle nest predation was also reported to be high at smaller rookeries in the Orango National Park, with estimates around 50% (Barbosa et al., 1998), and on the island of Canhabaque, where it reached 97% (Camará, 2023). Nile monitors were the main predator of green turtle eggs, similarly to what was previously described for the JVPMNP (Barbosa, Patrício, et al., 2018; Catry et al., 2002). These are generalist predators, with the ability to detect prey odours, that can adapt their foraging behaviour according to available food sources (Losos & Greene, 1988). Ghost crabs are important turtle egg predators globally (Barton & Roth, 2008; Marco et al., 2015; R. Martins et al., 2022; Witherington, 1999), yet at the JVPMNP they probably act as local opportunistic predators, considering the seldom observed predatory activity. One limitation of this study is that clutches on Poilão's neighbouring islands were primarily monitored during the initial 10 days after oviposition, covering only a portion of the incubation phase. Despite this limited observation period, predation levels on these islands were significantly higher than those on Poilão. If the uneven sampling had introduced any bias, it would likely have skewed the results in the opposite direction of the observed differences. On top of clutch predation, the predation of hatchlings can contribute to very low reproductive success on the islands of Cavalos, Meio and João Vieira.

Nest flooding varied across the JVPMNP, with Poilão experiencing 24.0% in 2013 and 12.0% in 2014. On the islands of Cavalos and Meio the rates were higher, 42.0% and 36.7%, respectively. Flooding at JVPMNP main islands occurs because of the low-lying setting of these nesting sites. This geographical characteristic can potentially enhance vulnerability to increases in sea level (Baker et al., 2006; Lyons et al., 2020) and coastal erosion (Siqueira et al., 2021) across all islands. Interestingly, not every nest affected by tidal washing experienced reduced hatching success. This appears to be linked to both the duration of the flooding event and the stage of development of the embryos. Limpus et al. (2020) observed that clutches either freshly laid or close to hatching suffered complete mortality in brief flooding events, a fate shared by all eggs subjected to extended periods of flooding (lasting 24 and 48 h). However, eggs in the mid-development phase (20−80%) exposed to short-term flooding (1−6 h) showed a notably high hatching success rate (Limpus et al., 2020). Recent studies have proposed that temporary flooding might help lower incubation temperatures, potentially increasing the production of male hatchlings (Laloë et al., 2016; S. Martins et al., 2022). Future nest excavation studies will be vital to further understanding the effects of flooding on green turtle nests at the JVPMNP. Nevertheless, we showed a very significant prevalence of flooding on the adjacent islands of Poilão, which is expected to increase under climate change scenarios (A. Dutton et al., 2015; Horton et al., 2014), emphasizing the constrained potential of these sites to support sea turtle reproduction in the future.

Although systematic surveys are not regularly conducted on Poilão's neighbouring islands due to logistical constraints, non-systematic field observations indicate that the results reported by our work are representative of other years. Our study revealed that clutch predation in Meio and João Viera was approximately 20 times higher than that at Poilão during the study years. Similarly, clutch flooding at Cavalos and Meio was about 2 to 3 times higher than that at Poilão during those years. The JVPMNP covers a relatively small area, making it highly probable that a specific annual event occurs on all the islands within its boundaries. Given that clutch predation and flooding on the other JVPMNP islands consistently exceeded those at Poilão, it is unlikely that we randomly selected poor years to survey the other islands.

3.5.3. SUITABLE NESTING SITES

Poilão is the island that currently gathers the best conditions for green turtle clutch survival within the JVPMNP. Nevertheless, this may change in the future due to population growth, to climate change-related threats, namely global mean SLR, or to a combination of both. If the nesting female population continues to increase, Poilão may start to experience moderate to high levels of nest destruction. Indeed, substantial nest destruction by subsequent nesting turtles has been found among green turtle (11%; Tiwari et al., 2006) and olive ridley turtle *Lepidochelys olivacea* (18%; Ocana et al., 2012) populations. In addition, SLR will further decrease the available nesting area at Poilão (predictions of 33.4 to 43.0% of beach loss by the year 2100 using a bath-tub model; Patrício et al., 2019), which will result in increased nest density and therefore an intensification of density-dependent nest destruction (Bustard & Tognetti, 1969; Girondot et al., 2002; Tiwari et al., 2006, 2010). Additionally, the packing of nests may enhance microbial infection in incubating eggs (Assersohn et al., 2021; Bézy et al., 2015), lowering clutch survival through embryo mortality. Collectively, these factors may lead to reduced hatching success at Poilão over the coming years.

If the nesting conditions at Poilão deteriorate, leading to increased clutch destruction, it is important for turtles to begin laying at the best alternative nesting sites available.

Cavalos seems to be that best alternative nesting site within the JVPMNP, primarily owing to its relatively low predation levels. However, it is important to note that Cavalos experiences considerable flooding. This is further compounded by its low-lying geography and the presence of an interior lagoon that connects to the sea during high tides, resulting in increased water content. The islands of Meio and João Vieira are currently heavily impacted by predation, but they have a higher profile and thus may be less vulnerable to SLR impacts. Nevertheless, coastal squeeze (i.e., beach narrowing; R. Silva et al., 2020) derived from erosion and rising sea levels, is expected to reduce the current available nesting area on all islands (Fish et al., 2005; Fuentes et al., 2010) and cause higher clutch mortality due to seawater inundation (Varela et al., 2019).

3.5.4. MANAGEMENT PRIORITIES AND RECOMMENDATIONS

Given the proportion of predated clutches reported in this study, the adoption of predation mitigation measures on the satellite colonies focused on the Nile monitor population should be considered, for example the use of protective mesh nets against terrestrial predators (Lovemore et al., 2020; O'Connor et al., 2017). Additionally, a study in Cavalos tested the use of a strong scent to disguise the natural odour of clutches, with some degree of success (Sampaio et al., 2022). The relocation of turtle eggs that are vulnerable to flooding to safer areas in the same beach has also been largely used to enhance clutch survival (Chacón-Chaverri & Eckert, 2007; Ilgaz & Baran, 2001; Margaritoulis, 1988; S. Martins et al., 2022). However, if clutch relocation was implemented, it would be important to leave some clutches in-situ to record hatching success and assess the impact of flooding.

As for other threats, although Cavalos does not have the same extent of traditional taboos as Poilão, it is also a sacred island where several activities are forbidden (agriculture, tree cutting, establishing fishing camps) and it is well protected (Catry et al., 2009). At present, it seems that the feral pigs do not pose a threat to green turtle clutches at Cavalos (Catry et al., 2018). Yet, if the green turtle population of the JVPMNP continues to grow, clutch predation by feral pigs would have to be re-evaluated (Engeman et al., 2016; Nordberg et al., 2019; Whytlaw et al., 2013). Enhanced protection of nesting turtles associated with heightened awareness specifically focused on turtle conservation could prove beneficial for Meio and João Vieira (e.g., Airaud et al., 2020). This becomes particularly crucial as turtle population growth continues and given the high risk of poaching during the slash-and-burn rice agriculture by the Bijagós people.

The limited occurrence of linkages between different islands of the JVPMNP from 2018 to 2020 was previously reported (Raposo et al., 2023). Furthermore, recent information from female green turtles flipper-tagged at Poilão and Meio in 2021 and 2022 has shown that exchanges between rookeries are maintained. In 2021, 1 out of 62 flipper-tagged turtles at Meio was resighted at Poilão (IBAP, unpub. data). It is noteworthy that these numbers reflect a limited survey effort per island for tagging and recapturing turtles, and thus the level of exchange between islands could be much higher than that detected. This inter-island exchange, coupled with the high clutch predation and/or flooding observed at Cavalos, Meio and João Vieira point to the existence of a source-sink dynamic (Dias, 1996; Pulliam, 1988), with Poilão acting as the source habitat and the remaining islands as sink habitats. It is well established that local threatened subpopulations can exhibit source-sink dynamics, where low-quality habitats (sinks) persist because they are sustained by the surplus individuals originated in high-quality habitats (sources; Pulliam, 1988). This has been documented among loggerhead turtles in Cabo Verde (Baltazar-Soares et al., 2020) and leatherback turtles *Dermochelys coriacea* on the Pacific coast of Costa Rica (Santidrián Tomillo et al., 2017). If confirmed, this dynamic would have significant demographic implications for the population nesting at the JVPMNP. Given the observed low reproductive success on alternative islands, there is a concern that Cavalos, Meio and João Vieira may not be able to serve as a potential replacement for Poilão if this site becomes unsuitable for nesting. We suggest that future studies assess the existence of a source-sink dynamic, to better inform conservation strategies and ensuring the long-term sustainability of the green turtle population in the JVPMNP.

Currently, monitoring efforts across JVPMNP islands are dictated by the significance of Poilão as a globally and locally important green turtle rookery. Cavalos is not monitored and there is a considerable gap in understanding sea turtle population ecology on this island. Hence, we propose that studies addressing green turtle reproductive success and associated threats are needed. In addition, research endeavours should focus on the role of density-dependent processes on the green turtle population at Poilão (e.g., Caut et al., 2006; Tiwari et al., 2006). Nevertheless, the costs and benefits linked to targeted conservation efforts in the JVPMNP must be considered. Decision-makers should consider the findings of this study, which identify Poilão as a probable source habitat that likely supports the other satellite colonies of the park, which are probable sink habitats.

The Bijagós Archipelago comprises 88 islands and islets (Catry et al., 2009) and prior research revealed that green turtles nest or nested in virtually all of its islands (Barbosa et al., 1998; Camará, 2023; Catry et al., 2009). For instance, nesting beyond the JVPMNP boundaries has been documented in the Orango National Park, with an estimate of 200-300 nests per year (Barbosa et al., 1998), and on Canhabaque Island, where 33 nests were recorded between August 20 to September 16, 2023 (Camará, 2023). Potentially, other islands of the Bijagós Archipelago can provide more favourable nesting conditions in the future, thus, conducting a comprehensive analysis of the green turtle reproductive success within the Bijagós Archipelago would be most beneficial.

CHAPTER 4

GREEN TURTLE NUTRIENT INPUT INTO A COASTAL ECOSYSTEM

NUTRIENT INPUT FROM GREEN TURTLE EGGS AND HATCHLINGS IN A WEST AFRICA ISLAND AND ITS NEARSHORE ENVIRONMENT

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Published: (2025). Nutrient input from green turtle eggs and hatchlings in a West Africa island and its nearshore environment. *Estuaries and Coasts*, 48, 64.
https://doi.org/10.1007/s12237-025-01500-9

4.1. ABSTRACT

Sea turtle nesting brings marine-derived nutrients into sandy beach ecosystems, potentially influencing their dynamics. We investigated nutrient input from green turtle *Chelonia mydas* eggs and hatchlings into coastal habitats in Guinea-Bissau, West Africa. We assessed 2 islands within the João Vieira-Poilão Marine National Park ('JVPMNP'), with contrasting sea turtle nesting density: very low (João Vieira) and very high (Poilão). On each island, we analysed stable isotopes of carbon and nitrogen in one pair of plant species (coinvine *Dalbergia ecastaphyllum* bush/baobab *Adansonia digitata* tree) and 2 pairs of predator species (tufted ghost crab *Ocypode cursor*/African rainbow crab *Cardisoma armatum* and sea catfish *Carlarius* spp./crevalle jack *Caranx hippos*). The first species in each pair is distributed closer to nesting sites, while the second is found further inland or offshore. Stomach content analysis was also conducted for fishes. Results supported nutrient input from turtle clutches benefiting the species living near nesting sites. Shoreline coinvines at Poilão had higher δ^{15}N (5.1 ± 3.2‰) compared to João Vieira (≈ 0‰), suggesting assimilation of turtle-derived ^{15}N. Shoreline tufted ghost crabs at Poilão had enriched δ^{15}N (15.2 ± 0.7‰ vs. João Vieira's 12.2 ± 1.1‰) and δ^{13}C (-13.4 ± 0.7‰ vs. João Vieira's -18.7 ± 1.4‰), likely reflecting predation upon eggs and hatchlings. Sea catfishes at Poilão frequently consumed unhatched turtle eggs washed into the sea (17% frequency of occurrence) and hatchlings (up to 27%). This study suggests that nutrient availability from turtle nests influences and supports shoreline plants and consumers at JVPMNP.

4.2. INTRODUCTION

Nutrients can be transported across ecosystem boundaries, connecting them (Doughty et al., 2016). Whilst physical vectors like wind and water contribute to nutrient transport between spatially distinct ecosystems, biotic vectors such as animals can also play an important role (Bauer & Hoye, 2014; McInturf et al., 2019; Polis et al., 1997; Vanni, 2002). Nutrient transport by animals can significantly influence nutrient cycling, ecosystem productivity, food web functioning, and support consumer populations within the recipient ecosystem (Subalusky & Post, 2019). For instance, animal-mediated nutrient transport from ocean to land is well described for seabirds (e.g., Adame et al., 2015; Anderson & Polis, 1998; González-Bergonzoni et al., 2017; Hawke & Holdaway, 2005; Sánchez-Piñero & Polis, 2000) and anadromous fish (e.g., Ben-David et al. 1998; Helfield and Naiman 2001; Gende et al. 2002; Reimchen et al. 2003; Koshino et al. 2013).

The range and relative nutrient input into the recipient ecosystem are influenced by the composition of its plant and animal communities. From a well-known example, in Alaska, salmon-derived nitrogen dispersed via brown bear *Ursus arctos* urine was detected up to 500 m from the stream in the foliage of white spruce trees *Picea glauca*, with nitrogen concentration decreasing with distance from the stream (Hilderbrand et al., 1999). Terrestrial nitrogen gain (foliage total nitrogen) via salmon biomass along a 500 m stream-to-forest transect was almost 20% (Hilderbrand et al., 1999). Riparian trees near anadromous Pacific salmon *Oncorhynchus* spp. spawning streams derive significant foliar nitrogen from salmon carcasses, with the highest values found within 25 m of streams and detectable up to 100 m (Helfield and Naiman 2001; Helfield and Naiman 2002). In the opposite direction, terrestrial invertebrates can contribute nutrients that sustain stream fish (Mason & Macdonald, 1982; Nakano et al., 1999). This dual cross-system nutrient flux can impact multiple trophic levels (e.g., Hocking & Reimchen, 2002).

In tropical, subtropical and warm temperate coastal regions, sea turtles are known to be important biotic vectors of nutrients between marine and coastal terrestrial ecosystems (Bouchard & Bjorndal, 2000). Nutrients derived from sea turtle eggs contribute to enhance vegetation growth along nesting beaches, aiding in shoreline stabilization and erosion control (Moss, 2017). Furthermore, the consumption of sea turtle eggs by terrestrial predators redistributes nutrients as these are subsequently dispersed through the predators' faeces, thus fostering ecosystem health and resilience (Moss, 2017). Previous research has highlighted the important role of sea turtle-mediated nutrient transport from marine to terrestrial ecosystems (Bouchard & Bjorndal, 2000; Hannan et al., 2007; Madden et al., 2008; Maros et al., 2006; H. B. Vander Zanden et al., 2012). For example, studies conducted on the east central coast of Florida, USA (Hannan et al., 2007) and in Tortuguero, Costa Rica (H. B. Vander Zanden et al.,

2012) investigated nutrient incorporation by different plants at beaches used by nesting green *Chelonia mydas* or loggerhead *Caretta caretta* turtles. These studies showed positive correlations between nest density and vegetation nitrogen isotopic signatures. Another study observed nitrogen enrichment in mole crickets *Scapteriscus didactylus*, terrestrial insects known to perforate leatherback turtle *Dermochelys coriacea* eggs (Maros et al., 2006); this increase was observed in individuals collected from nesting beaches compared to those collected near human settlements, suggesting that they had fed on turtle eggs (Maros et al., 2006). At Melbourne Beach, Florida, USA, it was estimated that 40% of the nitrogen derived from loggerhead turtle clutches was accessible to plants, detritivores and decomposers, while 26% was consumed by nest predators (Bouchard & Bjorndal, 2000). On Australia's north-west coast, an estimated 13% of the energy supplied by loggerhead turtle clutches into the beach environment became available to plants, detritivores and decomposers, 70% to terrestrial predators, and 8% returned to the ocean as hatchlings (Avenant et al., 2024).

The intricate ways in which nutrients are transported and assimilated within ecosystems can be investigated through indirect and direct methods, or a combination of both. Stable isotope analysis (SIA) is a valuable tool for investigating the flow of energy or mass through trophic levels and ecosystems (Ehleringer et al., 1986; Post, 2002). This technique relies on the premise that the isotopic ratios of consumers reflect those of their dietary sources through reasonably predictable patterns (Fry, 2006). SIA typically combines nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios. Nitrogen serves as a proxy for the consumer's trophic position as it gradually accumulates through the food chain, while carbon undergoes negligible changes along the food chain and is often used to distinguish original sources of dietary carbon, particularly when distinct carbon isotopic signatures characterize the sources (DeNiro and Epstein 1978; DeNiro and Epstein 1981; Peterson and Fry 1987; Post 2002).

SIA is also useful for tracking nutrient uptake by plants, including over different spatial and temporal scales (T. E. Dawson et al., 2002; Snyder et al., 2022). The $\delta^{15}N$ is generally used to identify the sources of nitrogen used by plants, such as atmospheric nitrogen fixed by nitrogen-fixing plants vs. soil nitrogen. In contrast, the $\delta^{13}C$ is commonly used to determine photosynthetic pathways (with C3 plants exhibiting lower $\delta^{13}C$ values than C4 plants), and to estimate water use efficiency, as well as to identify the sources of assimilated carbon (T. E. Dawson et al., 2002; Snyder et al., 2022).

While SIA can provide an integrated perspective on the assimilated dietary sources in animals over longer periods, stomach content analysis (SCA) offers direct evidence of recently ingested food items (Hyslop 1980; Pinnegar and Polunin 2000; Stergiou and Karpouzi 2002). The integration of SIA and SCA can offer a comprehensive approach to trophic studies, providing complementary insights into dietary patterns and enhancing the taxonomic resolution and reliability of dietary assessments (e.g., Gonzalez et al., 2021; Mantel et al., 2004; Parkyn et al., 2001).

The João Vieira-Poilão Marine National Park (hereafter 'JVPMNP'), located in the Bijagós Archipelago of Guinea-Bissau, West Africa, is an important marine protected area (MPA) that hosts one of the primary breeding aggregations of green turtles globally (Catry et al., 2009; Patrício et al., 2019). The park encompasses islands with undisturbed tropical seasonal forests immediately bordering the beach dunes, with zero to low human occupation, and heterogeneous green turtle nest densities (Raposo et al. 2024). These densities range from very high, with a mean of 2.04 nests m^{-2} on Poilão Island, to very low, with approximately 0.002 nests m^{-2} on João Vieira Island (Raposo et al. 2024). It is estimated that an average of 33,065 female turtles nested at Poilão each year between 2020 and 2022, laying around 3,912,960 eggs each year, yielding a total of 2,656,900 hatchlings (IBAP, unpub. data). In contrast, these estimates are much lower for João Vieira, with an average of 242 nests and 29,040 eggs per year (2020-2021, IBAP, unpub. data). Hatching success in João Vieira is unquantified, but clutch predation by Nile monitors *Varanus niloticus* is very high, affecting 76% of the clutches (Raposo et al. 2024). These discrepancies make this MPA an ideal location to study the nutrient contributions of sea turtles to sandy beach ecosystems. Here, we aimed to examine the input of nutrients from green turtle nesting activities into the coastal communities of the João Vieira-Poilão Marine National Park. We used 2 types of comparisons: i) of organisms of the same species collected on the islands with the lowest and highest sea turtle nest concentrations in the park; ii) of pairs of related species, one distributed along the shoreline and the second occurring both on the shoreline and further inland or, in the case of fishes, on offshore areas. We hypothesized that nutrient transport would be evident only in Poilão and would primarily be observed in the species occurring in closest proximity to sea turtle nesting sites.

4.3. MATERIALS AND METHODS

4.3.1. STUDY SITE

This study was conducted at the João Vieira-Poilão Marine National Park (JVPMNP), which lies on the southeast of the Bijagós Archipelago, in Guinea-Bissau, West Africa (N11°17', W15°58'; **Fig. 4.1**). The JVPMNP consists of 4 main islands: Poilão, João Vieira, Meio and Cavalos, characterized by low-lying sandy beaches and widely varying levels of green turtle nesting activity (Raposo et al. 2024). Poilão (10°52'N, 15°43'W; **Fig. 4.1**), covering an area of 43 ha, is the smallest island of the park and hosts the largest green turtle breeding aggregation in the entire archipelago (Catry et al., 2002, 2009), ranking among the top 6 globally (Patrício et al., 2019). At 900 ha in size, João Vieira (11°02'N, 15°38'W; **Fig. 4.1**) is the largest island but ranks lowest in number of nests among the JVPMNP islands (Barbosa, Patrício, et al., 2018). We selected João Vieira and Poilão as sites of low and high nest densities within the JVPMNP, respectively. At these sites, monitoring of sea turtle nesting activities is conducted annually by the Instituto da Biodiversidade e das Áreas Protegidas (IBAP) of Guinea-Bissau (Barbosa, Patrício, et al., 2018), the governmental institution responsible for biodiversity monitoring and management.

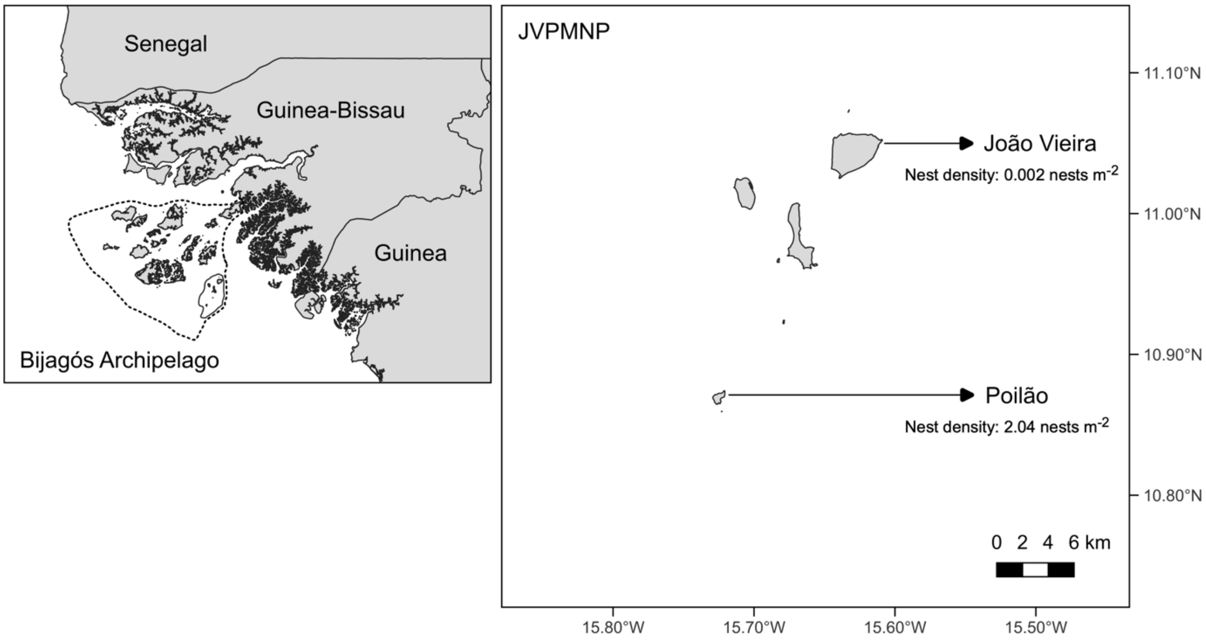

Fig. 4.1. Location of the João Vieira-Poilão Marine National Park (JVPMNP) depicted by the solid line within the Bijagós Archipelago, Guinea-Bissau, whose limits are shown by the dashed line. Green turtle nest densities were obtained from Raposo et al. 2024

4.3.2. SAMPLED SPECIES

At the JVPMNP, terrestrial predators of sea turtle eggs include crabs (e.g., ghost crabs *Ocypode* spp.), reptiles (e.g., Nile monitors) and birds (Palm-nut vultures *Gypohierax angolensis* and pied crows *Corvus albus;* Catry et al., 2002; Sampaio et al., 2022), while hatchlings are preyed upon by crabs (e.g., ghost crabs) and birds (Palm-nut vultures and pied crows*;* Carneiro et al., 2017; Catry et al., 2010; Rebelo et al., 2012). Marine predators of hatchlings include several species of fish (e.g., sea catfishes *Carlarius* spp., crevalle jack *Caranx hippos*, snappers *Lutjanus* spp., and Guinean barracuda *Sphyraena* spp.; Catry et al. 2010; IBAP, pers. comm.). To investigate the nutrient input from green turtle eggs and hatchlings into the coastal environment, we collected samples from 3 groups representing primary producers and terrestrial and marine predators of sea turtle eggs and hatchlings: 2 plant species, 2 crab species, and 2 fish species.

We chose the plant species coinvine (*Dalbergia ecastaphyllum*, Fabaceae, N = 36; **Table 4.1**) and baobab (*Adansonia digitata*, Malvaceae, N = 36; **Table 4.1**), due to their abundance along the beaches of both islands. Coinvines occupy littoral sand dune environments, whereas baobabs occur further inland, right behind the dune vegetation, where sea turtles also nest. Coinvine is a large shrub known to establish symbiosis in its root system with rhizobia for nitrogen fixation (Saur et al., 2000; Sotuyo et al., 2022). In contrast, baobab is a non-nitrogen-fixing tree.

Table 4.1. Number of samples collected per sampling group and species. Plant species include coinvines (*Dalbergia ecastaphyllum*) and baobabs (*Adansonia digitata*), crab species include tufted ghost crabs (*Ocypode cursor*) and African rainbow crabs (*Cardisoma armatum*), and fish species include sea catfishes (*Carlarius* spp.) and crevalle jacks (*Caranx hippos*)

Group	Species	Year	Location	Mouth gape	n
Green turtle eggs	*Chelonia mydas*	2021	Poilão	NA	19
		2022			20
		2023			5
Green turtle hatchlings	*Chelonia mydas*	2021	Poilão	NA	19
		2022			20
Plants	*Dalbergia ecastaphyllum*	2021	João Vieira	NA	5
			Poilão	NA	5
		2022	João Vieira	NA	5
			Poilão	NA	5
		2023	João Vieira	NA	8
			Poilão	NA	8
	Adansonia digitata	2021	João Vieira	NA	5
			Poilão	NA	5
		2022	João Vieira	NA	5
			Poilão	NA	5
		2023	João Vieira	NA	8
			Poilão	NA	8

Table 4.1. (continued)

Group	Species	Year	Location	Mouth gape	n
Crabs	*Ocypode cursor*	2021	João Vieira	NA	0
			Poilão	NA	6
		2022	João Vieira	NA	12
			Poilão	NA	12
	Cardisoma armatum	2021	João Vieira	NA	6
			Poilão	NA	6
		2022	João Vieira	NA	0
			Poilão	NA	0
Fishes	*Carlarius* spp.	2021	João Vieira	Restricted	8
				Wide	8
			Poilão	Restricted	1
				Wide	30
		2022	João Vieira	Restricted	0
				Wide	7
			Poilão	Restricted	1
				Wide	20
	Caranx hippos	2021	João Vieira	Restricted	2
				Wide	3
			Poilão	Restricted	4
				Wide	16
		2022	João Vieira	Restricted	0
				Wide	6
			Poilão	Restricted	4
				Wide	12
	Sardinella maderensis	2021	João Vieira	NA	10
			Poilão	NA	10
		2022	João Vieira	NA	10
			Poilão	NA	0

The selection of crab species was guided by their habitat preferences. Tufted ghost crabs (hereafter 'ghost crabs', *Ocypode cursor*, Ocypodidae, N = 30; **Table 4.1**) live and build their burrows on sandy beach littoral habitats typical of sea turtle nesting areas, whereas African rainbow crabs (*Cardisoma armatum*, Gecarcinidae, N = 12; **Table 4.1**) occur along the dunes as well as further inland. Ghost crabs are opportunistic omnivores and known predators of sea turtle eggs and hatchlings (Marco et al. 2015; Rae et al. 2019; Martins et al. 2021). A previous study documented the predation of green turtle hatchlings by this species at Poilão (Rebelo et al., 2012). African rainbow crabs are generally reported as herbivores (Lawal-Are & Gbewa, 2015; Ngo-Massou et al., 2021), but can also exhibit opportunistic omnivorous diets (Etchian et al., 2016; N'zi & Coulibaly, 2021; Olalekan & Lawal-Are, 2013), and are known to prey on sea turtle hatchlings (Kamel & Mrosovsky, 2005). On Poilão, this species is found in forested areas along the beaches where green turtles nest (Patrício et al., 2018), where they have been observed to prey on hatchlings (Catry et al., 2010).

Two predatory fish species, sea catfishes (*Carlarius* spp., Ariidae, N = 75; **Table 4.1**) and crevalle jack (*Caranx hippos*, Carangidae, N = 47; **Table 4.1**), were selected based on their ecology: sea catfishes are benthic and are frequently found nearshore, while crevalle jacks are highly mobile swimmers, usually found further offshore, although they also regularly forage in shallow coastal areas. Both species have been observed predating green turtle hatchlings at Poilão (IBAP, pers. comm.).

4.3.3. SAMPLING PERIOD

We collected samples of green turtle eggs and hatchlings, plants, crabs, and fishes for SIA. Additional fish samples were collected for SCA. The main green turtle breeding season in the JVPMNP runs from mid-June to mid-December, with peak nesting activity in August and September (Catry et al., 2002), while green turtle hatching takes place from mid-August to mid-February, with a peak between September and November. Sample collection of plants, crabs and fishes was conducted on both islands towards the end of the breeding season (October/November). This timing aimed to maximize the incorporation of the annual turtle clutches-derived nutrients into plant tissues and the turtle egg or hatchling nutrients into consumer tissues. Fishes were captured for SCA at both islands during the same period.

Green turtle eggs and hatchlings were exclusively collected at Poilão, considering previous research indicating that breeding turtles move between JVPMNP islands to nest (Raposo et al., 2023). Therefore, these samples are representative of the eggs and hatchlings of João Vieira. Sampling took place in 2021, 2022, and 2023.

Green turtle eggs and hatchlings

We collected addled green turtle eggs (hereafter 'eggs'), i.e., eggs containing yolk but exhibiting no visible signs of development (Hannan et al., 2007), as well as muscle tissue from dead hatchlings. During early morning beach surveys, we scoured the sand on Poilão for scattered turtle eggs and dead hatchlings that had not reached the ocean the previous night and were untouched by predators. Nest destruction by subsequent nesting turtles frequently result in eggs found exposed on the beach surface (Catry et al., 2009), a common occurrence at Poilão (Raposo et al. 2024).

Eggshells were removed using a sterile scalpel blade and only undeveloped egg contents were analysed. A small muscle sample from the flipper of each dead hatchling was also collected.

Vegetation

In 2021 and 2022, we selected 5 sampling sites per plant species per island, while in 2023 we selected 8 sampling sites. The selection of sampling sites was based on the existence of green turtle nests nearby; this corresponded to the entire Poilão shoreline, while in João Vieira we selected sites along the nesting areas. At each sampling site, we gathered 3 leaves from each plant species, ensuring consistency in leaf maturity and absence of herbivory. From these collected leaves, we randomly selected pieces and then combined them according to species and site. This process resulted in a single, finely mixed composite sample for each species at each site each year (H. B. Vander Zanden et al., 2012).

Crabs

Crabs were collected by hand from the beach in 2021 and 2022 during nightly exploratory surveys at non-fixed locations, with the exception of ghost crabs in João Vieira in 2022, which were sampled by digging their burrows due to difficulty in finding them active on the beach. All crabs were measured with a vernier caliper to the nearest 0.1 mm for carapace width ('CW', cm). Sex was not identified. Leg muscle tissue was collected from up to 2 legs, and all individuals were released shortly after handling.

Fishes

Fishes were captured from the beach in 2021 and 2022 using artificial bait (lures), cut bait, hook and line, and nets over 50 (October 31 to November 21, 2021) and 22 d (October 30 to November 20, 2022) in 2021 and 2022, respectively. During these periods, fishes were opportunistically caught. Net mesh sizes were 2.5 x 2.5 cm at Poilão and 1 x 1 cm or 2.5 x 2.5 cm at João Vieira. Shortly after capture and death by oxygen deprivation, we measured the fork length (FL, cm) of each fish to the nearest 1 mm using a flexible measuring tape.

Within the *Carlarius* genus, 2 species were identified through dental plate examination: rough-head sea catfish (*Carlarius latiscutatus*, Ariidae) and Guinean sea catfish (*Carlarius parkii*, Ariidae). These species have broadly similar diets consisting of crabs, fish, molluscs, and shrimp, but with different preferences for specific prey types, particularly crabs for *C. latiscutatus* and bivalves for *C. parkii* (Simier et al., 2021). However, since it was not possible to identify every individual at the species level, we present data for both species combined instead of estimating relative frequency. Prior research indicated Madeiran sardinella (*Sardinella maderensis*, Clupeidae) as a primary food source for crevalle jacks (Correia et al., 2017), so samples of this prey fish species were collected to assess differences between its isotopic ratios and the ones from green turtle eggs and hatchlings.

To ensure that we were capturing individuals capable of preying on turtle hatchlings, we classified predatory fish individuals into ‘restricted gape’ or ‘wide gape’ by determining the minimum size (i.e., FL) at which a hatchling could fit their mouth.

We collected samples of dorsal white muscle (hereafter ‘muscle’) of all fishes (Pinnegar and Pollunin 1999) and, when possible, blood from the heart region. We directly collected blood using a sterile syringe or a disinfected pointed spoon.

Stomach contents of sea catfishes were carefully removed and examined on-site. Identifiable contents were recorded in the field. Non-identifiable contents were preserved in 96% ethanol, transported to the laboratory, and classified using a stereomicroscope. Prey items were identified to the lowest taxonomic level possible using morphologic characteristics, and comparing them with a reference collection of vertebrae and other bones from a wide range of species compiled by different researchers at the Bijagós Archipelago (Correia et al., 2017). We examined the stomach contents of crevalle jacks on-site, and concluded that these were highly digested, making SCA impossible for this species.

4.3.4. STABLE ISOTOPE ANALYSIS

Both plant and animal (muscle and blood) tissues were thoroughly air-dried on-site for immediate preservation and stored in microvial tubes until subsequent processing to determine their $\delta^{15}N$ and $\delta^{13}C$. Tissue samples were oven-dried in the laboratory at 60°C for 24–48 h to remove moisture content. Vegetation samples were ground using a ball mill. As animal tissues were too sticky for the ground mill, they were ground into powder using a mortar and pestle. Since animal tissues with high lipid content frequently have more negative $\delta^{13}C$ values (Post et al., 2007), introducing a potential bias in the interpretation of δ^{13}C and trophic relationships, all animal samples underwent lipid extraction, a chemical process used to physically remove lipids from samples (Post et al., 2007). This began with the immersion of each sample in a 2:1 chloroform/methanol solution at a volume approximately 5 times that of the sample. After mixing for 30 s, the samples were allowed to settle for 30 min and then centrifuged for 10 min at 3400 rpm. The supernatant, which held solvent and lipids, was carefully removed. This process was repeated 3 to 5 times for each sample, until the supernatant was clear after centrifugation. Following lipid extraction, the samples were further dried in an oven at 60°C for 48 h to remove any residual solvent. A total of 4 to 5 mg and 0.75 to 1 mg of ground plant and animal tissue sample, respectively, were individually weighted into tin cups. The isotopic ratios were determined through continuous flow isotope mass spectrometry (CF-IRMS; P. J. H. Dunn & Carter, 2018), on a Sercon Hydra 20-22 (Sercon, UK) stable isotope ratio mass spectrometer, coupled to a EuroEA (EuroVector, Italy) elemental analyser for online sample preparation by Dumas-combustion. Delta values were calculated following the formula $\delta = [(R_{sample} - R_{standard}) / R_{standard}] * 1000$, where R represents the ratio between the heavier isotope and the lighter one (i.e., $^{15}N/^{14}N$ or $^{13}C/^{12}C$ ratio). δ^{15}N and δ^{13} values were calibrated against atmospheric nitrogen (N_2) and the Pee Dee Belemnite (PDB) scale, respectively. The reference materials used included IAEA N1, IAEA N2, USGS26, Glucose BCR no. 657, IAEA-CH7 and IAEA-C3. For plant samples, the laboratory quality control check used was Rice Flour, while for animal samples it was Bovine Liver Powder (commercial food additive). The uncertainty of the isotope ratio analysis, calculated using values from 6 to 9 replicates of laboratory standard interspersed among samples in every batch of analysis, was ≤0.2‰. The major mass signals of carbon and nitrogen were used to calculate total carbon (%C) and nitrogen (%N) contents for both plant and animal samples.

The timescale of isotopic incorporation, or turnover rate, reflects how quickly the consumers' tissues assimilate the dietary isotopic signal (Martínez del Rio et al., 2009; Thomas & Crowther, 2015). Vertebrate turnover rates vary widely, from a few days or weeks to months (Layman et al., 2012), influenced by tissue type, body size, growth and taxon (Martínez del Rio et al., 2009; M. J. Vander Zanden et al., 2015). For example, blood generally exhibits a rapid turnover rate compared to muscle (Thomas & Crowther, 2015). Knowledge of the turnover rates is therefore essential for interpreting stable isotope signatures, and selecting the appropriate biological tissue is key to investigate the period of interest (Carter et al., 2019). For crabs, we considered a muscle turnover rate (isotopic half-life) ranging from 4 to 6 mo, based on a timeframe established by previous research on marine arthropods (Bopp et al., 2023). There is a lack of isotopic turnover studies specific to our fish species (e.g., Papastamatiou et al., 2015). As proxies, we used turnover rates (isotopic half-life) from the muscle of subadult whitemouth croakers *Micropogonias furnieri* (δ^{15}N: 22.3 d, δ^{13}C: 17.7 d; Mont'Alverne et al., 2016). Considering these values, and the fact that in ectotherms blood has a rapid turnover rate compared to muscle (Buchheister & Latour, 2010; Warne et al., 2010), it is likely that the turnover rate of fishes blood will be faster.

4.3.5. DATA ANALYSIS

Two-way analyses of variance (two-way ANOVAs) were performed to evaluate the effects of location (= island), year and their interaction on δ^{15}N and δ^{13}C of all tissues of all species except African rainbow crabs. For fishes, this analysis was performed only for the 'wide gape' individuals. For African rainbow crabs, there is data from a single year, and we tested for differences in the isotopic signatures of African rainbow crabs between islands using Welch two-sample t-tests.

For each plant species we also used Welch two-sample t-tests to compare %N and %C between João Vieira and Poilão islands, considering data from all years. We examined the relation between δ^{15}N and %N of the plant tissues using simple linear regressions.

Since crabs with larger CW usually have larger chelae (Divine et al., 2017), we hypothesized that individuals with larger CW would potentially exhibit δ^{15}N values closer to those of green turtle hatchlings, as they are likely to capture and subdue larger prey items. The non-parametric Spearman's rank correlation was applied to test the associations between δ^{15}N and CW for both crab species.

We compared the isotopic signatures of crabs to those of their main purported prey – green turtle eggs and hatchlings, combined into one single group – using a method adapted from Meier et al. (2017). We applied the published mean trophic enrichment factor estimates of 3.4‰ for δ^{15}N and of 0.4‰ for δ^{13}C per trophic level (Post, 2002) to the mean isotopic signatures of turtle eggs and hatchlings. This allowed drawing, in the 2-dimensional isotopic space, the region occupied by "theoretical" crabs that would have been exclusively consuming this prey for longer than their isotopic turnover rate (Layman et al., 2012; Newsome et al., 2007). It is worth noting that the estimation of discrimination factors (i.e., the difference between the stable isotope values of an animal's tissue and its diet; Martínez del Rio et al., 2009) can be uncertain due to several factors like species, taxon, tissue, diet quality and isotopic composition, and the form of nitrogenous waste excretion (Martínez del Rio et al., 2009; M. J. Vander Zanden & Rasmussen, 2001; Vanderklift & Ponsard, 2003). Although species-specific estimates were not available, the broadly applicable estimates used in this study are suitable across various aquatic species and ecosystems (Post, 2002), still our results should be interpreted with caution.

We evaluated the associations between $\delta^{15}N$ and FL for each predatory fish species annually, using both muscle and blood tissue samples from all sampled fishes, including both 'restricted gape' and 'wide gape', with the non-parametric Spearman's rank correlation. Subsequent analysis focused solely on 'wide gape' fishes.

To visually compare the isotopic signatures of both predatory fishes to those of green turtle eggs and hatchlings, as well as to those of Madeiran sardinella, we applied the same methodology used for the crab species (see above), using previously published trophic enrichment factors (Post, 2002).

SCA was used to ascertain the importance of each prey item in the diet of both 'restricted gape' and 'wide gape' sea catfishes and facilitate comparisons between João Vieira and Poilão. Results were presented as frequency of occurrence (%) of each prey type, which represents the number of stomachs containing a particular prey item relative to the total number of sampled stomachs. In order to estimate the number of individuals of each prey item in the sea catfish's stomachs (hereafter 'numerical frequency'), we counted all discernible structures of each prey item. For example, a stomach containing one whole green turtle hatchling and 35 scutes was counted as containing 4 hatchlings – the whole individual and 3 more based on the 35 scutes, as each hatchling typically has 13 scutes. This allowed us to avoid over-representation of prey items in the sea catfish's diet. To assess potential size-related changes in the consumption of 'green turtle items' (i.e., the sum of green turtle eggs and hatchlings), 'benthic fauna' (i.e., the combined count of crabs not identified, marbled swimcrabs *Callinectes marginatus*, shrimps not identified, ophiuroids not identified, sea cucumbers not identified, and ball sea cucumbers *Phyllophorus* sp.), and 'nektonic fauna' (i.e., the total number of fish not identified, Madeiran sardinella *Sardinella maderensis*, and Lesser African threadfin *Galeoides decadactylus*), we used the non-parametric Spearman's rank correlation to evaluate the association between the numerical frequency of each of these prey items groups observed in the stomachs of sea catfishes and fish FL.

All statistical analyses were performed using R v4.2.2 software (R Core Team, 2022). Data are presented as mean ± standard deviation.

4.4. RESULTS

4.4.1. VEGETATION

There was a distinctly different interspecies pattern in $\delta^{15}N$ values. While coinvines displayed $\delta^{15}N$ values of approximately 0‰ in João Vieira and higher values in Poilão, baobabs exhibited similar values on both islands (**Table S4.1**, **Fig. 4.2**).

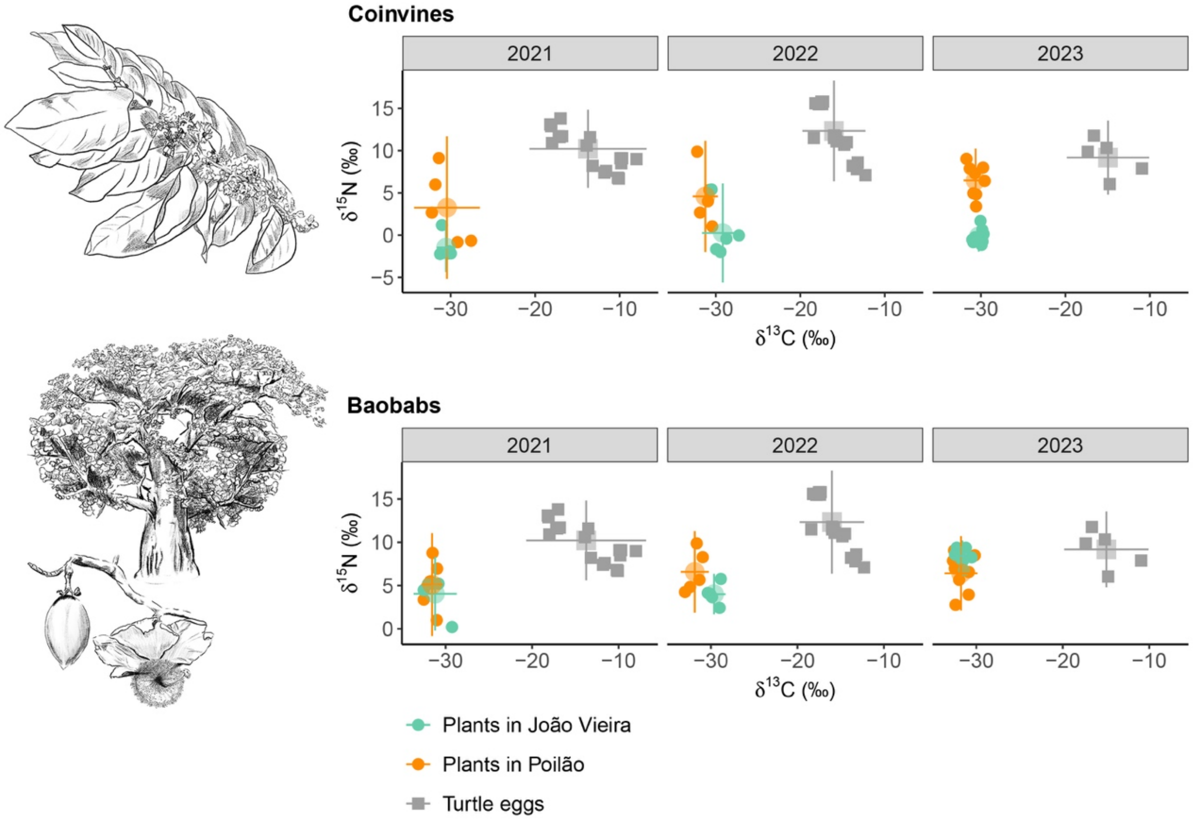

Fig. 4.2. Biplots of $\delta^{15}N$ and $\delta^{13}C$ values for coinvines *Dalbergia ecastaphyllum* and baobabs *Adansonia digitata*, along with green turtle *Chelonia mydas* eggs, by year at João Vieira and Poilão

Regarding coinvines, only the location had a significant effect on $\delta^{15}N$ (two-way ANOVA $F_{1,30} = 40.97$, $p < 0.001$) and $\delta^{13}C$ (two-way ANOVA $F_{1,30} = 4.39$, $p = 0.045$). For baobabs, both the year (two-way ANOVA $F_{2,30} = 6.98$, $p = 0.003$) and the interaction between location and year (two-way ANOVA $F_{2,30} = 4.31$, $p = 0.023$) significantly influenced their $\delta^{15}N$ values. Moreover, location (two-way ANOVA $F_{1,30} = 7.56$, $p = 0.010$), year (two-way ANOVA $F_{2,30} = 3.67$, $p = 0.038$) and their interaction (two-way ANOVA $F_{2,30} = 5.05$, $p = 0.013$) significantly affected their $\delta^{13}C$ values.

There were no differences in %N (coinvines: $t_{32.77}$ = -0.66, *p* = 0.26; baobabs: $t_{27.35}$ = 1.35, p = 0.91) and %C (coinvines: $t_{34.00}$ = -0.66, *p* = 0.26; baobabs: $t_{30.01}$ = -0.48, *p* = 0.32) between islands for either plant species. Overall, increases in foliar %N did not correspond to significant increases in δ^{15}N, with the exception of coinvines in Poilão in 2021 (adjusted r^2 = 0.78, *n* = 5, $F_{1,3}$ = 14.98, *p* = 0.031; **Table S4.2**, **Fig.4. 3**) and baobabs in João Vieira that same year (adjusted r^2 = 0.80, *n* = 5, $F_{1,3}$ = 17.42, *p* = 0.025; **Table S4.2**, **Fig.4. 3**). However, there was also a significant negative relation between δ^{15}N and %N for baobabs in Poilão in 2021 (adjusted r^2 = 0.90, *n* = 5, $F_{1,3}$ = 35.17, *p* = 0.010; **Table S4.2**).

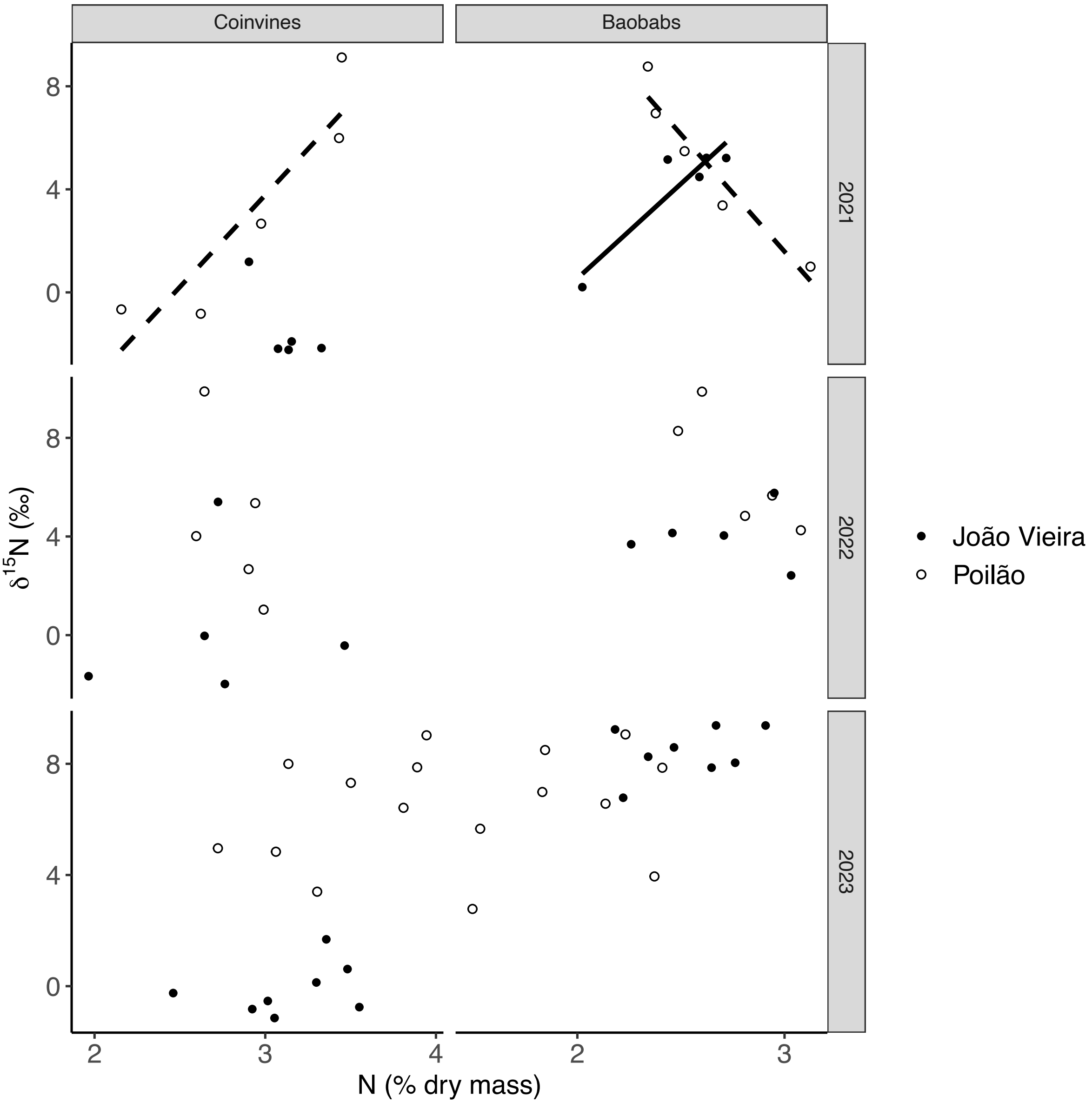

Fig. 4.3. Scatterplot showing the relation between foliar nitrogen isotopic ratio (δ^{15}N) and nitrogen content (%N) for coinvines *Dalbergia ecastaphyllum* and baobabs *Adansonia digitata*, by year in João Vieira and Poilão. The solid and dashed lines indicate significant relations in João Vieira and Poilão, respectively

4.4.2. CRABS

Overall, ghost crabs had a mean (± standard error, SE) CW of 4.6 ± 0.1 cm (range: 2.4–5.8 cm), while African rainbow crabs had a mean (± SE) CW of 8.3 ± 0.5 cm (range: 5.9–12.5 cm).

Ghost crabs exhibited enriched δ^{15}N and δ^{13}C values in Poilão, compared to João Vieira (**Table S4.1**, **Fig. 4.4**), whereas African rainbow crabs showed lower ratios of both isotopes than green turtle eggs or hatchlings on both islands (**Table S4.1**, **Fig. 4.4**).

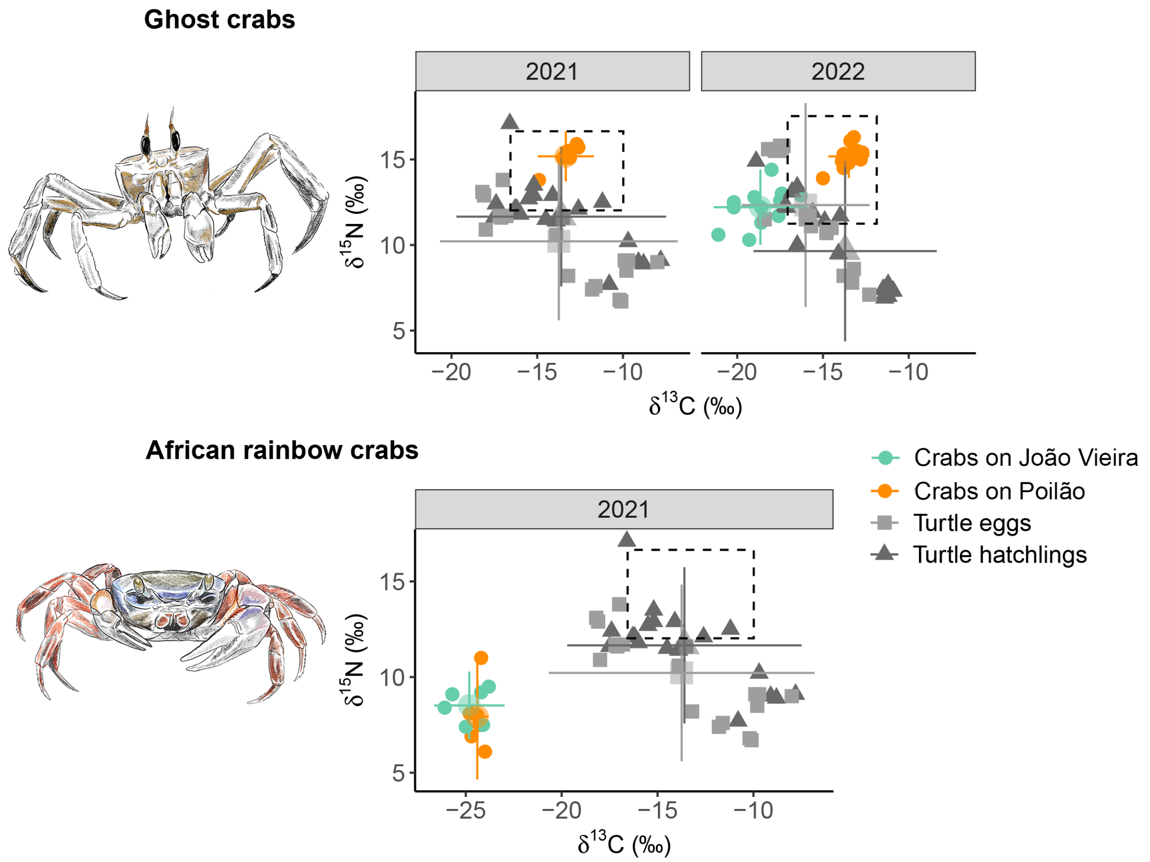

Fig. 4.4. Biplots of δ^{15}N and δ^{13}C values for tufted ghost crabs *Ocypode cursor* and African rainbow crabs *Cardisoma armatum*, along with green turtle *Chelonia mydas* eggs and hatchlings, by year at João Vieira and Poilão. The dotted boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings, based on mean trophic enrichment factors of 3.4‰ for δ^{15}N and 0.4‰ for δ^{13}C

Location significantly affected both δ^{15}N (two-way ANOVA $F_{1,27} = 80.95$, $p < 0.001$) and δ^{13}C (two-way ANOVA $F_{1,27} = 182.84$, $p < 0.001$) for ghost crabs. On the other hand, there were no significant differences in δ^{15}N (two sample t-test = 0.75, $p = 0.76$) and δ^{13}C (two sample t-test = -1.04, $p = 0.17$) between islands for African rainbow crabs. The isotopic signatures of ghost crabs in Poilão in both years were contained within the isotopic niche of a theoretical green turtle consumer (**Fig. 4.4**). The isotopic niches of ghost crabs in João Vieira and African rainbow crabs on both islands did not overlap with that of a turtle consumer (**Fig. 4.4**). In 2022, we found a significant positive correlation between $\delta^{15}N$ and CW for ghost crabs (Spearman rank correlation, rs = 0.46, *n* = 24, *p* = 0.025; **Table S4.3**). In 2021, we did not find significant correlations between $\delta^{15}N$ and CW for either crab species (**Table S4.3**).

4.4.3. FISHES

In 2021 and 2022, a total of 75 sea catfishes were sampled, with a mean FL of 34.4 cm (range 24.8–66.1 cm). Of these, 65 individuals met the 'wide gape' criterion (**Table 4.1**), with a minimum FL of 29.6 cm. Among these, 17 (26.2%) were found to have green turtle eggs (eroded or unhatched yet intact eggs likely washed out into the sea) and/or hatchlings in their stomachs. In the same years, 47 crevalle jacks were caught, with a mean FL of 47.1 cm (range 30.7–88.0 cm). Of these, 37 crevalle jacks were classified as 'wide gape' (**Table 4.1**), with a minimum FL of 37.0 cm, of which only 1 (2.7%) had green turtle hatchling remains in its stomach. None of the fishes from either species that were classified as 'restricted gape' had turtle contents in their stomachs.

In 2021, a significant positive correlation was observed between $\delta^{15}N$ and FL for blood samples of the entire sea catfish sample (Spearman rank correlation, rs = 0.73, *n* = 12, *p* = 0.007; **Table S4.4**). Conversely, a significant negative correlation was found in blood samples of crevalle jacks (Spearman rank correlation, rs = -0.52, *n* = 17, *p* = 0.031; **Table S4.4**). When considering only 'wide gape' fishes, both predatory fish species exhibited higher mean $\delta^{15}N$ values and similar mean $\delta^{13}C$ values compared to those of green turtle eggs and hatchlings, whether for muscle or blood samples (**Table S4.1**, **Fig. 4.5**, **Fig. 4.6**). In sea catfish muscle tissue, both $\delta^{15}N$ (two-way ANOVA $F_{1,61}$ = 117.07, *p* <0.001) and $\delta^{13}C$ (two-way ANOVA $F_{1,61}$ = 15.50, *p* <0.001) were significantly influenced by the year, but not by location, while in blood samples $\delta^{15}N$ was affected by location (two-way ANOVA $F_{1,29}$ = 7.19, *p* = 0.012). For crevalle jacks, $\delta^{13}C$ in both muscle (two-way ANOVA $F_{1,33}$ = 14.70, *p* <0.001) and blood samples (two-way ANOVA $F_{1,33}$ = 7.06, *p* = 0.013) were significantly influenced by location. Sea catfishes shared the isotopic niche of an exclusive green turtle consumer on both islands, whether muscle or blood samples were assessed, except for muscle samples of individuals captured on both islands in 2021 (**Fig. 4.5**). In contrast, crevalle jacks' isotopic signatures did not overlap with that isotopic niche (**Fig. 4.6**). In both years, crevalle jacks captured at Poilão had isotopic signatures that corresponded with those of a theoretical Madeiran sardinella consumer (**Fig. 4.6**).

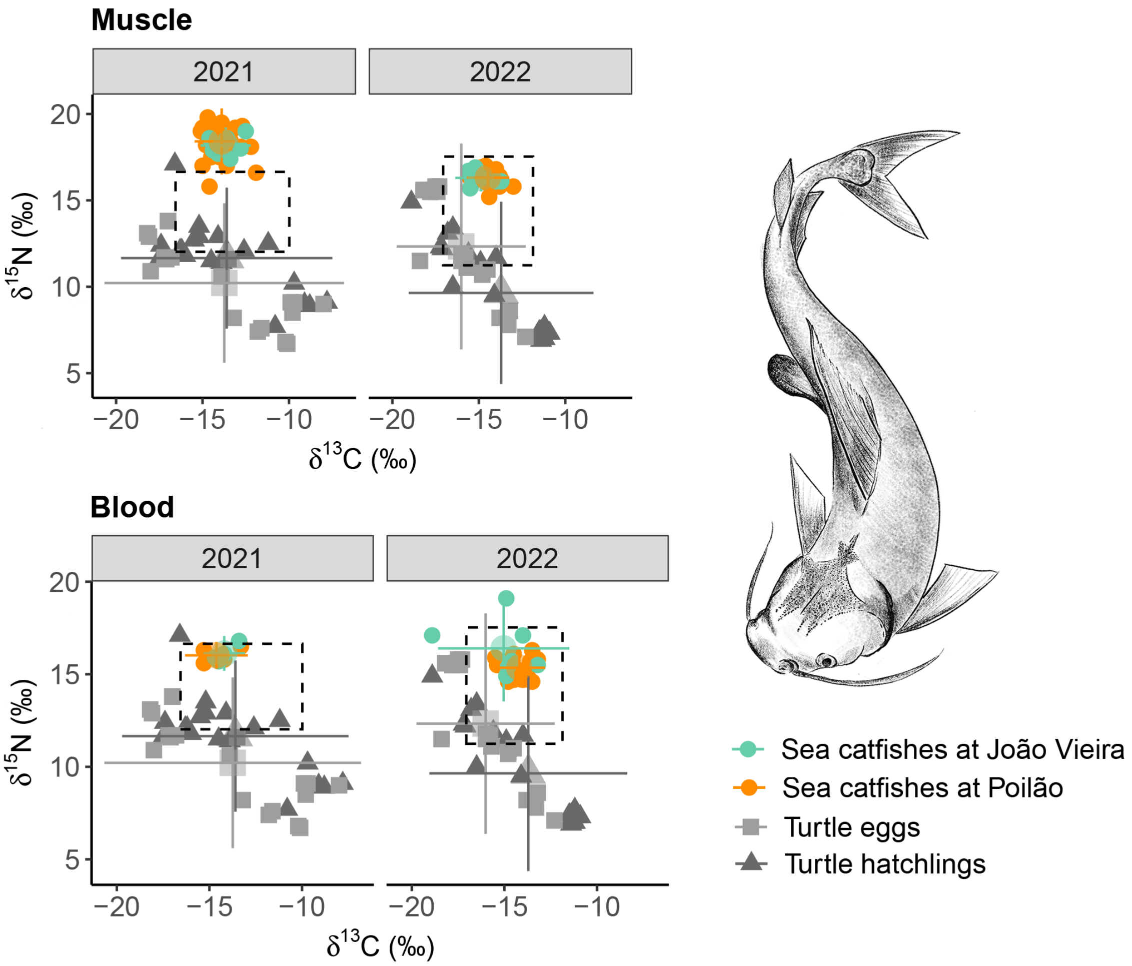

Fig. 4.5. Biplots of $\delta^{15}N$ and $\delta^{13}C$ values for muscle and blood samples of sea catfish *Carlarius* spp., along with green turtle *Chelonia mydas* eggs and hatchlings, by year at João Vieira and Poilão. Only fish classified as 'wide gape' were used here. The dotted boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings, based on mean trophic enrichment factors of 3.4‰ for $\delta^{15}N$ and 0.4‰ for $\delta^{13}C$

The majority of sea catfish stomach contents exhibited either partial or advanced digestion, posing challenges for precise identification of contents. Unidentified crabs and fish species (including not identified fish, Madeiran sardinella, and the Lesser African threadfin) were the dominant prey for 'restricted gape' and 'wide gape' sea catfishes captured at João Vieira and Poilão (**Fig. 4.7**, **Fig. 4.8**). Additionally, 'wide gape' sea catfishes captured at Poilão exhibited a high frequency of consumption of green turtle eggs and hatchlings (**Fig. 4.8**). We found a significant positive correlation between the numerical frequency of green turtle items in their stomachs and FL in 2021 (Spearman rank correlation, rs = 0.60, *n* = 38, *p* <0.001; **Table S4.5**).

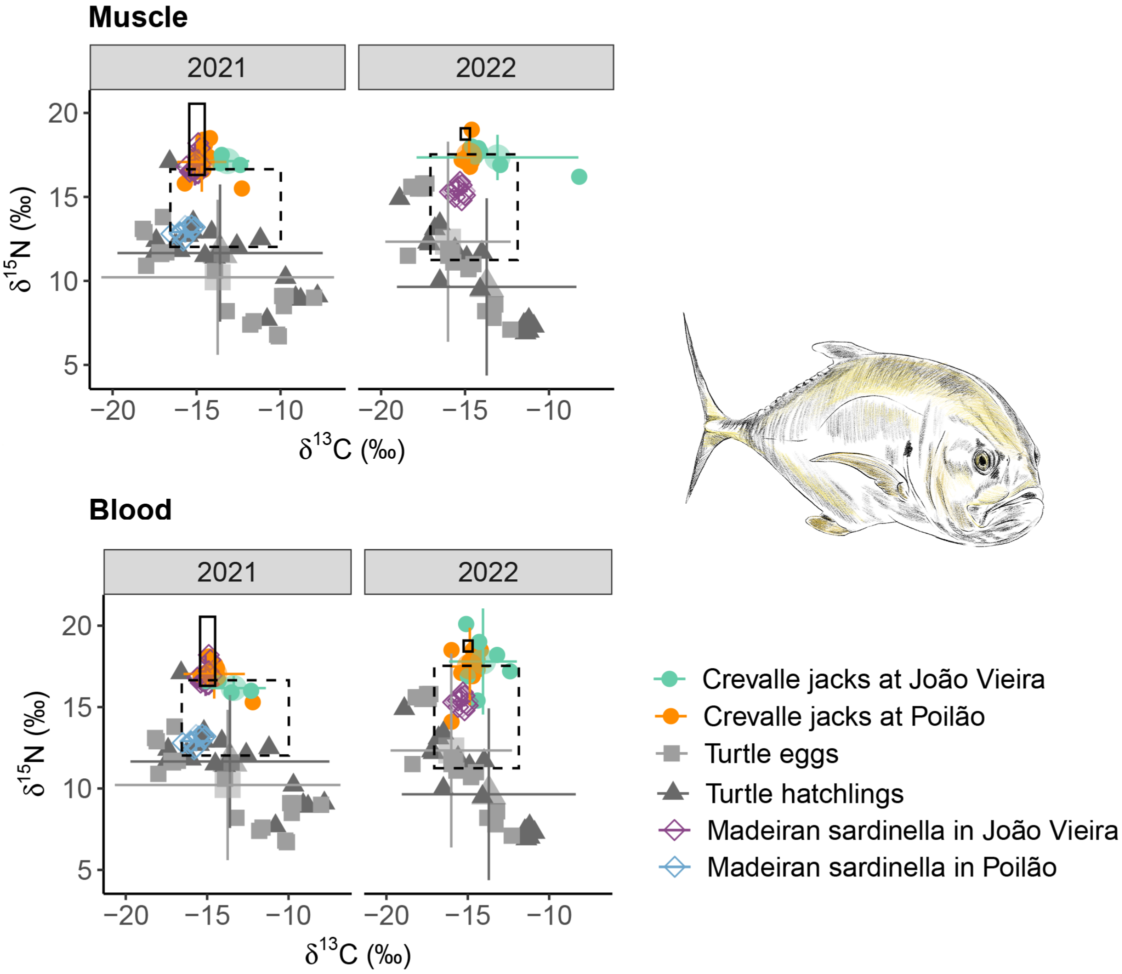

Fig. 4.6. Biplots of $\delta^{15}N$ and $\delta^{13}C$ values for muscle and blood samples of crevalle jack *Caranx hippos*, along with green turtle *Chelonia mydas* eggs and hatchlings, and Madeiran sardinella *Sardinella maderensis*, by year at João Vieira and Poilão. The Madeiran sardinella is a locally present year-round species often consumed by jacks. Only fish classified as 'wide gape' were used here. The boxes represent the expected range in isotopic values of a consumer feeding on green turtle eggs and hatchlings (dotted boxes) and on Madeiran sardinella (solid boxes), based on mean trophic enrichment factors of 3.4‰ for $\delta^{15}N$ and 0.4‰ for $\delta^{13}C$. The relatively small sample size used in this study most likely limits the narrow region defined in the isotopic biplot for Madeiran sardinella

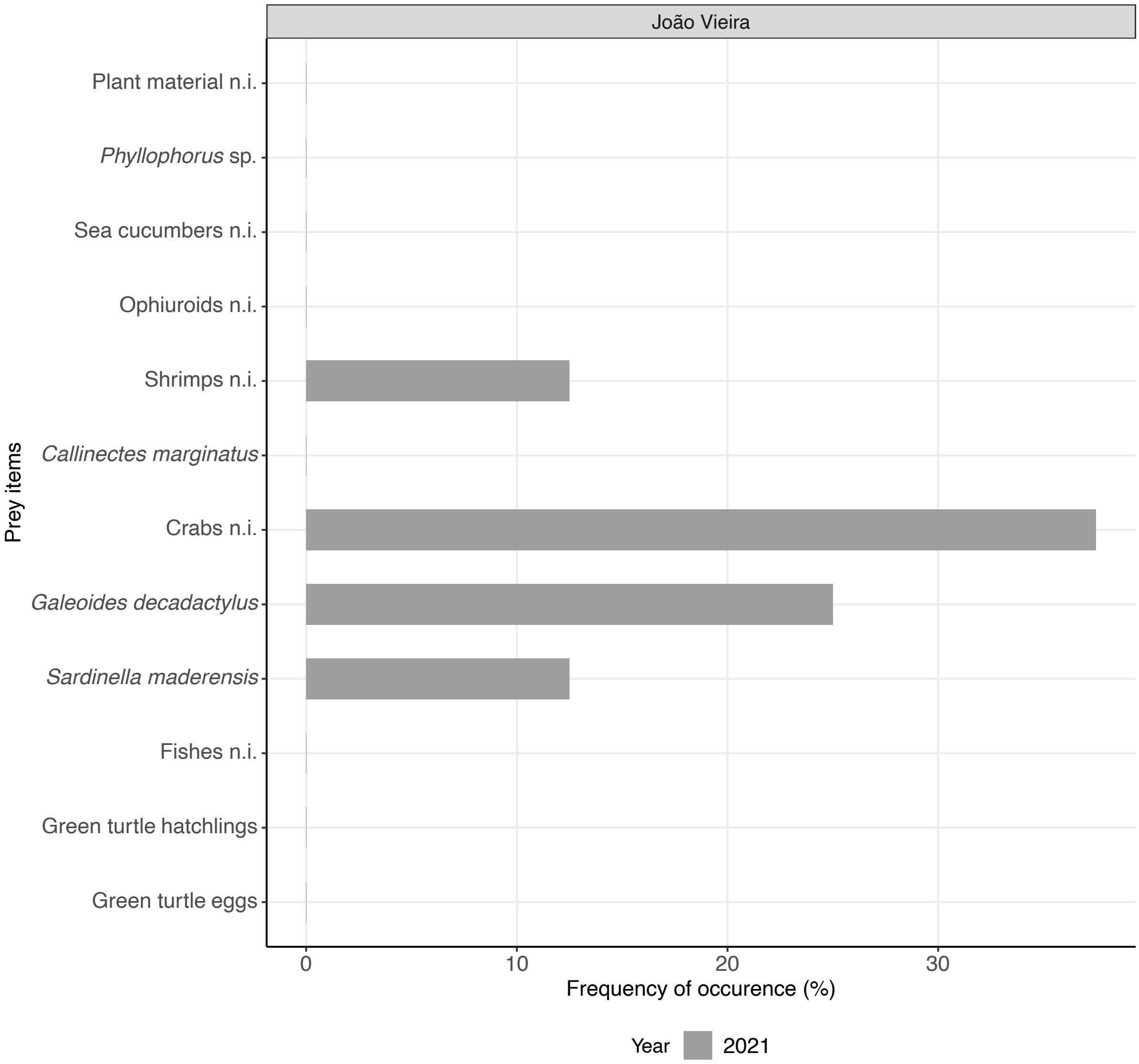

Fig. 4.7. Frequency of occurrence (%) of prey items in the stomachs of sea catfishes *Carlarius* spp. classified as 'restricted gape'. 'n.i.' denotes not identified

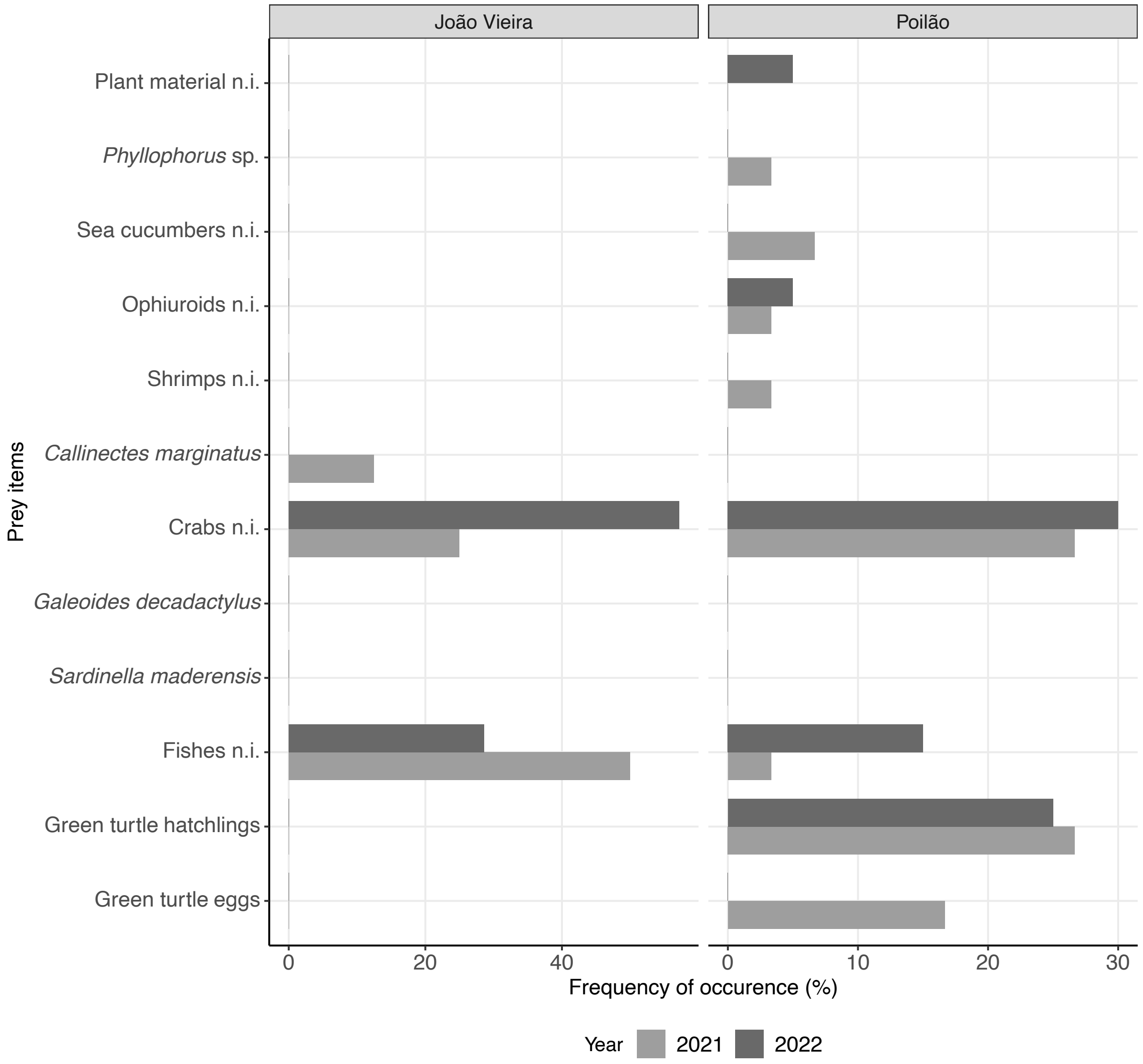

Fig. 4.8. Frequency of occurrence (%) of prey items in the stomachs of sea catfishes *Carlarius* spp. classified as ‘wide gape’. ‘n.i.’ denotes not identified

4.5. DISCUSSION

We examined the nutrient input from green turtle eggs and hatchlings into some of the commonest species of the coastal communities of the João Vieira-Poilão Marine National Park in Guinea-Bissau. We compared sites with low and high sea turtle nest densities and pairs of organisms from the same species group (plants, crabs and fishes) – one with a closer to shore distribution and the other frequenting more inland or further offshore areas. Our objective was to examine the importance of sea turtle nutrients across the coastal terrestrial and marine habitats. We found evidence of nutrients very probably derived from green turtle clutches over time, but only in species that reside directly or very near sea turtle nesting sites and at the highest sea turtle nest density island.

4.5.1. GREEN TURTLE NUTRIENT UPTAKE BY PLANTS

Green turtles in Poilão nest towards the top of the frontal dune, with a significant proportion of clutches laid either on the vegetation border or under the vegetation (36%; Patrício et al., 2018), especially under coinvine bushes and baobab trees. In general, the observed differences in foliar $\delta^{15}N$ and %N patterns between the 2 species are consistent with previous findings. Nitrogen-fixing plants, such as coinvines, typically have $\delta^{15}N$ values approaching 0‰ due to symbiotic atmospheric nitrogen fixation (Craine et al., 2015; R. D. Evans, 2001; D. Robinson, 2001), whereas their %N is often higher than that of non-fixing plants (R. D. Evans, 2001). This pattern differs from baobabs, which rely only on soil-derived nitrogen sources.

The contrasting $\delta^{15}N$ values of coinvines between the low and the high sea turtle nest density sites suggest that nitrogen was acquired from different sources across islands. Approximately 70 to 80% of the nitrogen in a nitrogen-fixing plant is fixed by the rhizobia, while the remainder is absorbed by the root system (Bruning & Rozema, 2013). Thus, the higher $\delta^{15}N$ values of coinvines in Poilão may have been influenced by the isotopic composition of nitrogen sources in the soil, such as nutrients derived from green turtle clutches. Research has shown that the roots of the beachgrass *Ammophila breviligulata* can absorb nutrients exuded from the eggs of the diamondback terrapin *Malaclemys terrapin* (Stegmann et al., 1988), and that plant roots invaded 23% of loggerhead turtle nests in Melbourne Beach, Florida, USA (Bouchard & Bjorndal, 2000). Nitrogen fixation by plants may be more energy-consuming than using soil nitrogen, as symbiotic bacteria need carbohydrates from the host plant for ammonia production (Hannan et al., 2007). Hence, in nutrient-poor environments like sandy beaches, coinvines may benefit from the increased availability of marine-derived nitrogen from sea turtles. Here, coinvines' $\delta^{15}N$ values were enriched at the high density sea turtle nest location. Similarly, enriched foliar $\delta^{15}N$ values were observed in nitrogen-fixing plants in other studies comparing high to low density sea turtle nesting sites (Hannan et al., 2007).

Biotic nitrogen input typically promotes plant growth in nutrient-limited environments (Leghari et al., 2016). In terrestrial ecosystems, bird guano-derived nutrients enhance plant growth (e.g., Burger et al., 1978; Magnússon et al., 2014; Sánchez-Piñero & Polis, 2000), and salmon-derived nutrients promote riparian forest growth along the aquatic-terrestrial interface (e.g., Helfield and Naiman 2001; Helfield and Naiman 2002). Furthermore, nitrogen availability often limits productivity in several ecosystems (Elser et al., 2007; LeBauer & Treseder, 2008; Vitousek & Howarth, 1991). However, despite the potential availability of nitrogen from the high density of sea turtle nesting sites, with the exception of coinvines in Poilão in 2021, there was no correlation between $\delta^{15}N$ and %N in either of the plant species studied. This may happen, for example, if plants responded to the highest nitrogen availability by growing more leaves, flowers and/or fruits, rather than enriching their leaf nutrient content.

4.5.2. GREEN TURTLE NUTRIENT UPTAKE BY CRABS

Ghost crabs' $\delta^{15}N$ values, and their alignment with the trophic niche of a theoretically exclusive green turtle consumer in Poilão, but not in João Vieira, indicate extensive feeding on green turtle eggs and/or hatchlings on the first island, where these resources are highly abundant. Our results were expected, since ghost crabs have been documented preying on sea turtle eggs and hatchlings on several sea turtle nesting sites (e.g., Playa Grande, Costa Rica; Santidrián Tomillo et al., 2010; Onslow Beach, North Carolina, USA; Peterson et al. 2013; Boa Vista Island; Marco et al., 2015; R. Martins et al., 2022; Diego Garcia, Chagos Archipelago, Indian Ocean; H. J. Stokes et al., 2024; and on the north-west coast of Australia; Avenant et al., 2024), including Poilão (Rebelo et al., 2012). Additionally, as hypothesized, ghost crabs with larger carapace width had higher $\delta^{15}N$ values, suggesting their increased potential to capture and subdue larger prey, such as green turtle hatchlings.

On the other hand, the isotopic ratios of African rainbow crabs on both islands suggest that they do not often rely on green turtle eggs or hatchlings as food sources (although they have been confirmed to predate or scavenge hatchlings, at least occasionally; Catry et al., 2010). Furthermore, the relatively low $\delta^{15}N$ signatures, similar to those of green turtle eggs, suggest that they are mainly primary consumers at the JVPMNP.

It should be noted, however, that the isotopic signatures of crabs captured in October and November possibly reflect dietary information since April or June, which falls before the peak of green turtle nesting activity at the JVPMNP. Therefore, the isotopic signal of crabs may partly reflect the assimilation of sea turtle-derived carbon and nitrogen, diluting their effect and yielding a conservative isotopic signature for ghost crabs.

4.5.3. GREEN TURTLE NUTRIENT UPTAKE BY FISHES

The blood $\delta^{15}N$ values of sea catfishes differed between João Vieira and Poilão, but both matched the isotopic niche of a green turtle consumer. This match with both the low- and high-density sea turtle nesting sites raises the possibility that other prey (untested) may be responsible for this overlap. Thus, sea catfishes perhaps feed on a range of prey at both islands that have isotopic signals similar to those of green turtle eggs and hatchlings. Earlier studies highlighted the importance of crabs and fishes in the diet of generalist predator sea catfishes (Faye et al., 2012; Simier et al., 2021). Similarly, stomach contents of sea catfishes at Poilão showed reliance on crabs and fishes, and the positive correlation between $\delta^{15}N$ and fork length suggests that larger sea catfishes consumed prey at higher trophic levels. Among that diversity of prey, other fish or crabs may be the providers of isotopic signatures similar to those of sea turtles, hindering the ability to differentiate sea turtle hatchling consumption between both islands. Nevertheless, stomach contents confirmed that sea catfishes at Poilão consume a high quantity of green turtle hatchlings, not observed at João Vieira. Importantly, the availability of turtle resources may be essential for other local predatory fish, for example snappers, as they are known to feed on green turtle hatchlings (Catry et al., 2010).

Crevalle jacks are described as large predators primarily preying on other fishes (Fagade & Olaniyan, 1973; Jefferson et al., 2022; Kwei, 1978), mainly clupeids within the Bijagós Archipelago (Correia et al., 2017). Their $\delta^{13}C$ values varied by location, suggesting different resource use between islands. Overall, their isotopic signatures did not match those of an exclusive sea turtle predator at either island. However, the overlap between their isotopic signatures and those of an exclusive Madeiran sardinella predator was high on both islands (and higher than of an exclusive sea turtle predator), suggesting that this prey may be much more frequently consumed than sea turtle hatchlings. This preference for Madeiran sardinella was reported by Correia et al. (2017). Crevalle jacks with larger body sizes, however, had lower $\delta^{15}N$ values, suggesting that they were feeding at a lower trophic level. This can be due to the consumption of hatchlings by larger specimens. However, generally our stable isotope results suggested that crevalle jacks do not extensively rely on green turtle eggs and hatchlings at the JVPMNP. Furthermore, we only found sporadic consumption of green turtle hatchlings at Poilão based on on-site stomach content observations.

In this study, we used different tissue types (muscle and blood) to represent distinct timeframes of dietary information. Like crabs, the isotopic signatures of fishes are also likely conservative, as they partly reflect the diet consumed prior to the integration of sea turtle isotopes. Crevalle jacks showed a high dietary overlap between short-term (blood) and long-term (muscle) signatures. This may be related to a diet dominated by clupeids (e.g., Madeiran sardinella; Correia et al., 2017), that are highly abundant year-round in the Bijagós Archipelago. In contrast, sea catfishes exhibited variation in short-term and long-term consumption in 2021, though the causes for this variation remain to be ascertained.

4.5.4. FINAL CONSIDERATIONS

Our results, along with prior research, indicate that sea turtles play an important role in supplying nitrogen to coastal plants, which may be particularly significant in nutrient-depleted sandy beach environments. Additionally, we observed that turtle eggs and hatchlings make an important contribution to the local food web. These ecological functions should be considered in management strategies. For instance, clutch relocation is a widely practiced and globally prevalent conservation method. However, the ecological importance of sea turtle clutches for coastal ecosystems should be taken into account if relocations become extensive. Green turtles transport nutrients from the ocean to the land at Poilão. While we did not quantify the extent of this shoreward transport along a coast-to-forest transect, our findings demonstrate that turtle-derived nutrients are concentrated near the coastal dune habitat. This is evident from the isotopic signals detected in coinvines and ghost crabs. Although not observed during this study, the assimilation of these nutrients could promote plant growth, contributing to shoreline stabilization (Moss, 2017) and influence the abundance of herbivorous invertebrates (Ebeling et al., 2022; Martínez et al., 2024; Tomasula et al., 2023).

Nitrogen input from green turtle clutches can potentially affect plant community composition (Avolio et al., 2014; Firn et al., 2019; Harpole et al., 2016). Green turtle nesting at Tortuguero, Costa Rica, has been shown to affect the dominant plant species, with different species prevailing in areas of low and high sea turtle nest densities (H. B. Vander Zanden et al., 2012). Plant growth, in turn, can benefit sea turtles. Sea turtles exhibit temperature-dependent sex determination, with high incubation temperatures yielding more females and low incubation temperatures yielding more males (Jensen et al., 2018; Santidrián Tomillo & Spotila, 2020; Tanner et al., 2019). A healthy coinvine population along the dunes of Poilão may help provide cooler incubation conditions, promoting the production of male hatchlings (Patrício et al., 2017). This can be particularly important in the context of future global warming (Patrício et al., 2021).

Green turtles also directly provide nutrients to consumers, influencing community dynamics. The availability of green turtle eggs and hatchlings shapes the foraging behaviour of ghost crabs in the JVPMNP, and potentially sea catfishes, as local reports indicate an increase in sea catfish abundance at Poilão during the green turtle breeding season (IBAP, pers. comm.). A study by Carneiro et al. (2017) found that Palm-nut vultures prey on green turtle eggs or hatchlings at Poilão and João Vieira. The vultures appear to migrate from João Vieira to Poilão during the green turtle breeding season to capitalise on the temporal abundance of green turtle resources (Carneiro et al., 2017). Comparing the relative abundance of predators (e.g., ghost crabs and sea catfishes) between islands and assessing the level of predation would provide valuable insights into hatchling survival, supporting conservation and management efforts at Poilão.

The number of green turtle nests in Poilão has increased in the last 20 years (Barbosa, Patrício, et al., 2018; A. Broderick & Patrício, 2019), with an average annual estimate of 32,608 nests over a recent 3-year period (Raposo et al. 2024). As sea turtles introduce substantial nutrients to sandy beaches (Bouchard & Bjorndal, 2000), these nutrients may have further effects throughout the sandy beach ecosystem. On Poilão Island, the $\delta^{15}N$ values of green turtle eggs and hatchlings may have a limited geographic range, but their ecological impact likely extends beyond this spatial range. Nutrients derived from turtle eggs and hatchlings probably not only contribute to the isotopic signature of their predators, such as ghost crabs, but also to increased biomass production and progeny among those predators. This, in turn, creates a secondary effect, as the progeny of predators – who may exhibit diluted or absent $\delta^{15}N$ turtle signatures – distribute nutrients more broadly across the ecosystem. Such secondary nutrient redistribution supports increased food availability and enriches the ecosystem beyond the spatial extent directly indicated by the $\delta^{15}N$ values of green turtle eggs and hatchlings. On the other hand, nutrient redistribution by sea turtles should be increasingly considered. By supporting a variety of organisms through nutrient redistribution, as observed in seabirds (Hentati-Sundberg et al., 2020), sea turtles help maintain high biodiversity levels. Therefore, their conservation contributes to the thriving of other species in the ecosystem.

CHAPTER 5

SEA TURTLE SITE FIDELITY

Cheila Raposo

SEA TURTLE SITE FIDELITY: CURRENT KNOWLEDGE AND FUTURE DIRECTIONS

Cheila Raposo

5.1. ABSTRACT

Site fidelity, i.e., consistently returning to a previously visited area, is a known behavioural tendency among sea turtles. This helps to ensure the use of beaches suitable for clutch incubation, increasing the reproductive fitness of adult turtles and contributing to population survival, as well as improving foraging by providing prior knowledge about the spatial and temporal availability of food sources. Nevertheless, plasticity in site fidelity can be also advantageous, as it allows the colonisation of new nesting beaches or relocation to an alternative feeding location when in face of adverse circumstances. Information on sea turtle site fidelity is important for informed conservation planning and management since it identifies repeatedly used areas that can be prioritized for protection. I conducted a review of sea turtle site fidelity, including site fidelity to (i) nesting beaches, (ii) inter-nesting habitats, (iii) male site fidelity to breeding grounds, and (iv) foraging grounds, to help guide future research. Thus far, most research has focused on site fidelity to the nesting beach, followed by foraging grounds. The most studied species are loggerhead *Caretta caretta* and green *Chelonia mydas* turtles, with tagging and tracking being the preferred methodologies employed. Generally, site fidelity and plasticity are common traits among sea turtle species. I highlight knowledge gaps and challenges in understanding site fidelity in sea turtles, in addition to strategies that can be adopted to overcome these. I also suggest research priorities to direct future research. Importantly, I emphasize the need for a standardized concept of site fidelity that should be used in future studies. Furthermore, to facilitate and improve the efficiency of the search process in future work, I suggest the inclusion of the term ‘fidelity’ as a keyword in studies that do not have site fidelity as their main topic.

5.2. INTRODUCTION

Many mobile marine species perform periodic migrations between breeding and non-breeding grounds because their breeding and feeding locations can be widely separated geographically, sometimes by thousands of kilometres (Alerstam & Bäckman, 2018; Clay et al., 2017; Egevang et al., 2010; Le Boeuf et al., 2000; Shillinger et al., 2008; Stone et al., 1990). These animals can exhibit fidelity to particular sites, both within and between breeding or foraging seasons (e.g., Bannister et al., 2016; Casale et al., 2023; Kelly et al., 2010; Limpus et al., 1984; Oksanen et al., 2014). Sea turtles are an example of such species, with complex life history patterns that include long-distance movements occurring during different developmental and reproductive life stages (Bolten, 2003; Musick & Limpus, 1997). All 7 sea turtle species are known to make periodic breeding migrations between foraging and breeding grounds, typically every 2 to 4 years (Schroeder et al., 2003; Southwood & Avens, 2010). Additionally, they can incur in seasonal movements related to foraging or overwintering behaviour (A. C. Broderick et al., 2007; Hawkes et al., 2007; Southwood & Avens, 2010).

Site fidelity, the phenomenon of animals frequently returning to previously visited areas (Bell et al., 2009; Switzer, 1993), has been well documented in sea turtles since early research (Caldwell, 1962; Mortimer & Portier, 1989). However, while this term (‘site fidelity’) is often employed in the context of returning to a known breeding or foraging area (e.g., Esteban et al., 2015; Nordmoe et al., 2004), several studies use it as a broader concept that includes residency, which implies the permanence within a relatively restricted geographic area (e.g., Hardy et al., 2023; Naro-Maciel et al., 2018; Nivière et al., 2018; Pillans et al., 2022; Tanabe, Cochran, Williams, et al., 2023; L. D. Wood et al., 2017). Some studies also combine both concepts (Sanchez et al., 2024). In addition, sea turtles are known for their ability to return to the region where they hatched to breed, a behaviour called natal philopatry or natal homing (Cury, 1994; Greenwood, 1980). This homing behaviour, which has been extensively demonstrated through genetic assessments (Allard et al., 1994; Bowen et al., 1989; Bowen & Karl, 2007; P. H. Dutton et al., 2013; Levasseur et al., 2019; Meylan et al., 1990; Naro-Maciel et al., 2014), can be considered a specific form of site fidelity outside the scope of this chapter.

The tendency of sea turtles to return to the same area repeatedly over time has been examined both during the breeding and foraging seasons (e.g., Gredzens & Shaver, 2020; Read et al., 2014; Shimada et al., 2021). Throughout the breeding season, turtles can exhibit site fidelity to the nesting beach (repeated nesting or nesting emergences within a restricted geographic range; Patino-Martinez et al., 2023), fine-scale site fidelity (repeated nesting or emergence on the same area of the nesting beach at a finer scale of tens of metres; Hamann et al., 2022), inter-nesting site fidelity (returning to the same in-water areas between successive nesting events; Raposo et al., 2023), and male site fidelity to breeding grounds (returning to the same mating area; James et al., 2005). Foraging site fidelity occurs when turtles return to their previous feeding location (A. C. Broderick et al., 2007). In general, site fidelity behaviour helps ensure reproduction in suitable habitats, reduces energy costs of locating new sites and improves foraging due to the predictability of the quality of food sources (Hays & Scott, 2013; Shimada et al., 2020). However, plasticity in these behaviours exists, with turtles sometimes deviating from site fidelity (e.g., K. L. Stokes et al., 2015). This allows turtles to adapt to changing environmental conditions (Carreras et al., 2018), as dynamic sandy beaches may change unpredictably across nesting seasons (Hilterman & Goverse, 2007; Kelle et al., 2007), making long-term suitability uncertain. In such environments, turtles frequently use bet-hedging strategies (Cunnington & Brooks, 1996; Lovich et al., 2015; Refsnider & Janzen, 2010; Rollinson & Brooks, 2007), prioritizing long-term reproductive output by spreading their clutches across multiple locations to increase the overall reproductive success (Lovich et al., 2015). If conditions at the primary nesting site deteriorate, less faithful turtles may explore alternative habitats, improving their chances of successful reproduction (Schofield, Hobson, Lilley, et al., 2010). Likewise, foraging grounds may have long-term suitability and knowledge of previous conditions at localised sites outweighs the risk of relocation (Shimada et al., 2020). However, relocation may be necessary if the initial foraging ground is impacted by natural (Arias-Ortiz et al., 2018) or anthropogenic (H. B. Vander Zanden et al., 2016) threats.

Selective pressures likely favour returning to sites that support survival and successful reproduction (Shimada et al., 2020) if these locations continuously provide the necessary resources for it. In fact, an essential evolutionary advantage of being site-faithful is knowledge of on-site conditions, either at breeding or foraging grounds. Comparatively, relocating to a new location may be riskier due to the absence of knowledge of resource availability or habitat conditions.

At both spatial and temporal scales, site fidelity can influence the long-term survival of clutches and the expected primary hatchling sex ratios. For example, clutch mortality is lower on beaches with cooler sand temperatures, whereas female-biased hatchling sex ratios (e.g., Hays, Mazaris, et al., 2014; King et al., 2013; Monsinjon et al., 2019) can occur on beaches with higher sand temperature. Furthermore, site fidelity can have negative effects if turtles consistently nest on beaches with moderate to severe poaching instead of geographically distinct beaches without this anthropogenic threat. This reasoning applies to other human-induced threats. Similarly, foraging site fidelity in unsuitable areas will have negative effects compared to continued feeding in areas with adequate resources.

Several methodologies may be used to assess sea turtle site fidelity, including (i) recaptures of external (via flipper tags) or internal (via passive integrated transponders, PIT tags) tagged turtles (e.g., Limpus et al., 1992; N. Pilcher & Chaloupka, 2013), (ii) tracking devices (e.g., Marcovaldi et al., 2010), (iii) stable isotope analysis (SIA, e.g., Bradshaw et al., 2017; Haywood et al., 2020), and (iv) genetic analyses (e.g., Wright et al., 2012). Overall, flipper tagging allows to identify long-term patterns of movement (Read et al., 2014), but it requires a significant survey effort since large numbers of tagged turtles are needed as well as extensive fieldwork to successfully resight them. Furthermore, recapture and reporting biases may occur (Godley et al., 2008). In contrast, satellite tracking can provide near real-time, detailed information about movements, but this is an expensive technology that frequently results in small sample sizes (Godley et al., 2008). Recurrence in foraging grounds is sometimes evaluated by combining satellite tracking with SIA, which allows to identify distinct isotopic niches from specific foraging grounds. This, in turn, allows untracked female turtles to be assigned to these putative foraging grounds (Ceriani et al., 2015). SIA can also be utilised independently to infer potential foraging grounds with distinct isotopic ratios. These potential foraging grounds can then be verified by tracking selected individuals to locate the foraging ground linked with the original isotopic signatures (Bradshaw et al., 2017). Genetic tools, such as molecular genetic markers like microsatellite loci, can be used in parentage analysis and to extract information regarding site fidelity (Wright et al., 2012).

The behaviour and movement patterns of breeding and foraging sea turtles have been studied for many years. Despite this considerable research, there are still uncertainties in the degree of site fidelity to breeding and foraging grounds in some sea turtle species or populations. This has been identified as a research priority for sea turtle management and conservation (Godley et al., 2008; Hamann et al., 2010; Hays & Hawkes, 2018; Rees et al., 2016). Given this, I will present a review of the literature on sea turtle site fidelity, focusing on site fidelity to (i) nesting beaches, (ii) inter-nesting habitats, (iii) male site fidelity to breeding grounds, and (iv) foraging grounds, considering repeated returns to previously visited areas. The review summarises the existing knowledge on sea turtle site fidelity, highlights gaps and challenges, and outlines research priorities to improve our understanding of this behaviour, aiding future sea turtle research, management and conservation efforts.

5.3. METHODS

I examined research on sea turtle site fidelity during the breeding and foraging stages, focusing on published peer-reviewed papers between 1983 and 2023. I did not include book chapters, MSc theses or PhD dissertations. I conducted a literature search on Web of Science using the search terms: ‘fidelity’ and ‘sea turtle’ or ‘marine turtle’ and ‘nesting’ or ‘foraging’ not ‘natal homing’. To identify additional literature, I conducted a similar search in Google Scholar and applied the snowball search strategy to find further references cited in the relevant papers, as well as in those that cited them. The PRISMA 2020 diagram flow was used to illustrate the search process (**Fig. 5.1**; Page et al., 2021). The titles and abstracts of the search results were screened to select those relevant to this study. Full texts were subsequently screened, and the exclusion criteria applied were: (a) papers addressing ‘residency’ and not real site fidelity, i.e., turtles staying in the same geographic area for extending periods, whether inter-nesting or foraging areas, (b) papers that only presented molecular genetic data without linking it to site fidelity, and (c) all papers that did not reported site fidelity on sea turtles. The selected papers were then classified by behavioural stage, with ‘breeding’ indicating site fidelity during the breeding period, including site fidelity to nesting beaches, inter-nesting habitats and male site fidelity to breeding grounds, and ‘foraging’ reflecting site fidelity to foraging grounds during the foraging period. The papers were also categorized based on the location of site fidelity, species, life stage, sex, habitat, ocean basin, and methodology used to assess site fidelity.

To assess the effectiveness of the search process, I estimated precision. Precision indicates the proportion of retrieved articles that are actually relevant, and it was calculated as follows: number of relevant retrieved articles divided by the total number of retrieved articles (Gusenbauer & Haddaway, 2020).

5.4. SUMMARY OF THE KEY RESEARCH TOPICS ON SEA TURTLE SITE FIDELITY

The search terms used in Web of Science identified 175 papers, while Google Scholar’s literature search combined with the snowball strategy yielded 47 papers (**Fig. 5.1**). During screening, many studies (28%, 50 out of 180) were excluded because they addressed residency and not site fidelity, as defined in this study. Generally, high precision indicates that the search returns mostly relevant articles with a few irrelevant ones (Gusenbauer & Haddaway, 2020).

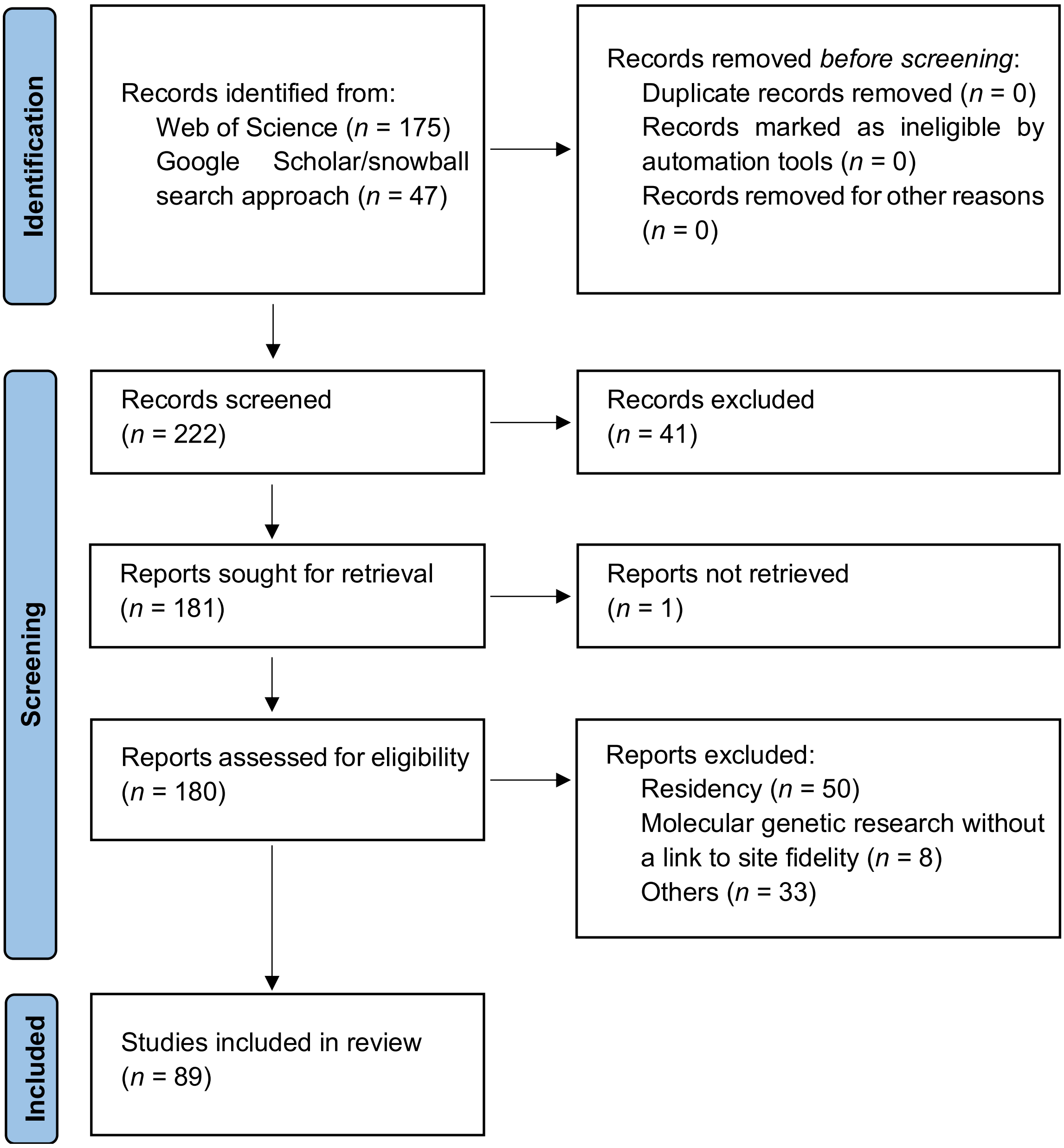

Fig. 5.1. PRISMA 2020 flow diagram for sea turtle site fidelity

The search terms used in this study returned nearly half (49%) of the retrieved articles as relevant, suggesting that the terms were broad, which increased the likelihood of capturing irrelevant articles alongside relevant ones. This could be owing to the specific definition of site fidelity utilised here – i.e., in the strict sense of return to a previously visited site – compared to a vague definition in the literature, often including residency at breeding or foraging sites without evidence of these sites having been visited previously.

A total of 89 peer-reviewed papers were considered relevant (**Fig. 5.1**, **Fig. 5.2**). From these, 73% (65 out of 89) and 36% (32 out of 89) were assigned to the breeding and foraging stages, respectively (**Fig. 5.2**). Over the last 2 decades, there has been an overall increase in research on sea turtle site fidelity during the breeding and foraging stages (**Fig. 5.2**). For both behavioural stages, a significant number of studies have reported site fidelity (breeding stage: 60%, 39 out of 65; foraging stage: 59%, 19 out of 32; **Fig. 5.3**), as opposed to the use of novel sites (no fidelity; breeding stage: 5%, 3 out of 65; foraging stage: 3%, 1 out of 32; **Fig. 5.3**). Several studies have found both sea turtle site fidelity and plasticity (plasticity; breeding stage: 35%, 23 out of 65; foraging stage: 38%, 12 out of 32; **Fig. 5.3**).

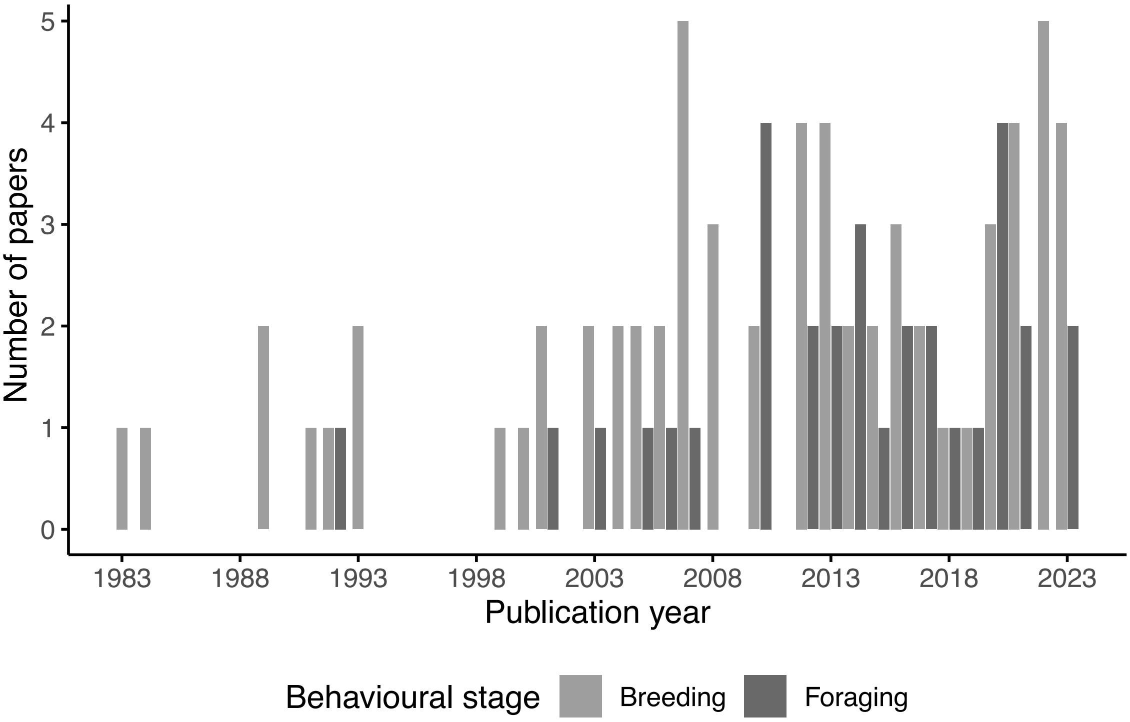

Fig. 5.2. Number of peer-reviewed papers on sea turtle site fidelity published between 1983 and 2023 by behavioural stage (breeding: *n* = 65; foraging: *n* = 32). The total number of papers in both behavioural stages categories surpass the total number of papers reviewed (*n* = 89) because 8 papers encompassed both behavioural stages

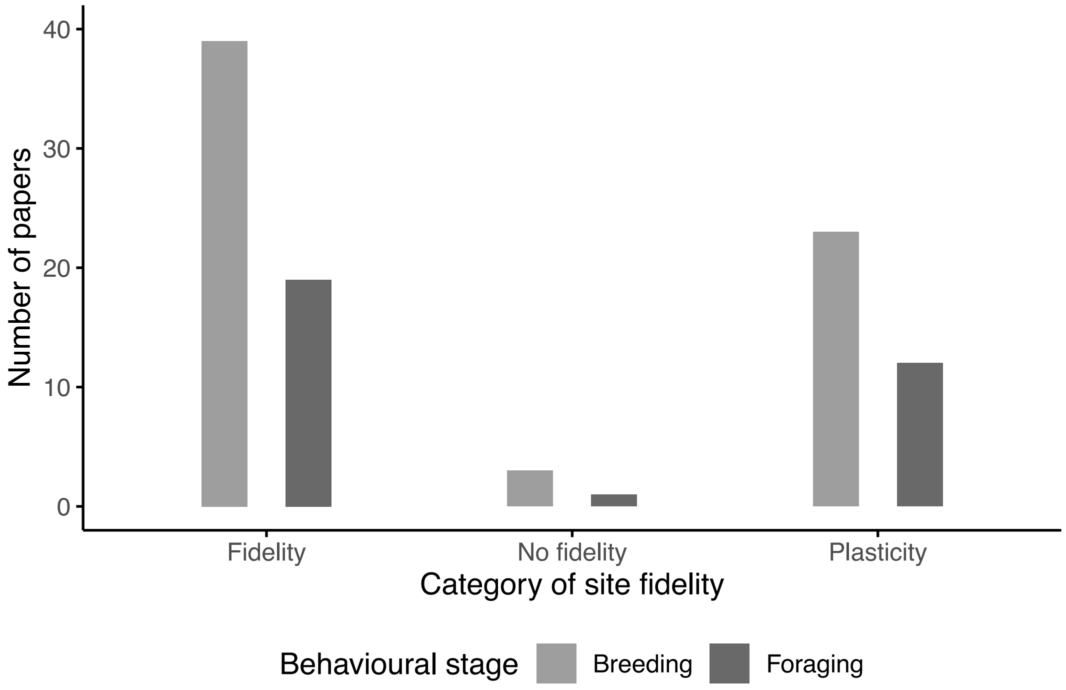

Fig. 5.3. Number of peer-reviewed papers by each category of site fidelity in sea turtles

Considering both behavioural stages, a substantial amount of research has focused on site fidelity to the nesting beach, followed by foraging grounds, with less attention given to inter-nesting habitats and male site fidelity to breeding grounds (**Fig. 5.4**). The limited number of studies reporting male site fidelity to breeding grounds is linked to the fact that most research has been targeting adult female turtles, with fewer studies on adult males or immature turtles (**Fig. 5.4**). In the past 40 years, loggerhead *Caretta caretta* and green *Chelonia mydas* turtles have been the most extensively studied, while Kemp’s ridley *Lepidochelys kempii*, flatback *Natator depressus* and olive ridley *Lepidochelys olivacea* turtles were the less researched species (**Fig. 5.4**). In terms of specific environment, there has been an approximately comparable number of papers focusing on coastal beaches and oceanic islands, with less research focused on other habitats such as estuaries and coastal sounds (**Fig. 5.4**).

Concerning the geographic distribution, many papers have focused on the Atlantic, followed by the Pacific, Caribbean Sea and the Mediterranean Sea, still the Gulf of Mexico and the Indian Ocean have also received some attention (**Fig. 5.4**). Site fidelity on sea turtles has been mostly determined using flipper tags (but sometimes PIT tags) and tracking devices, with additional or occasionally complementary approaches, such as SIA (**Fig. 5.4**). It is worth noting that the total number of papers in other categories (except for life stage and sex), and in both categories of behavioural stage, may exceed the total number of papers reviewed because some papers reported multiple options or stages.

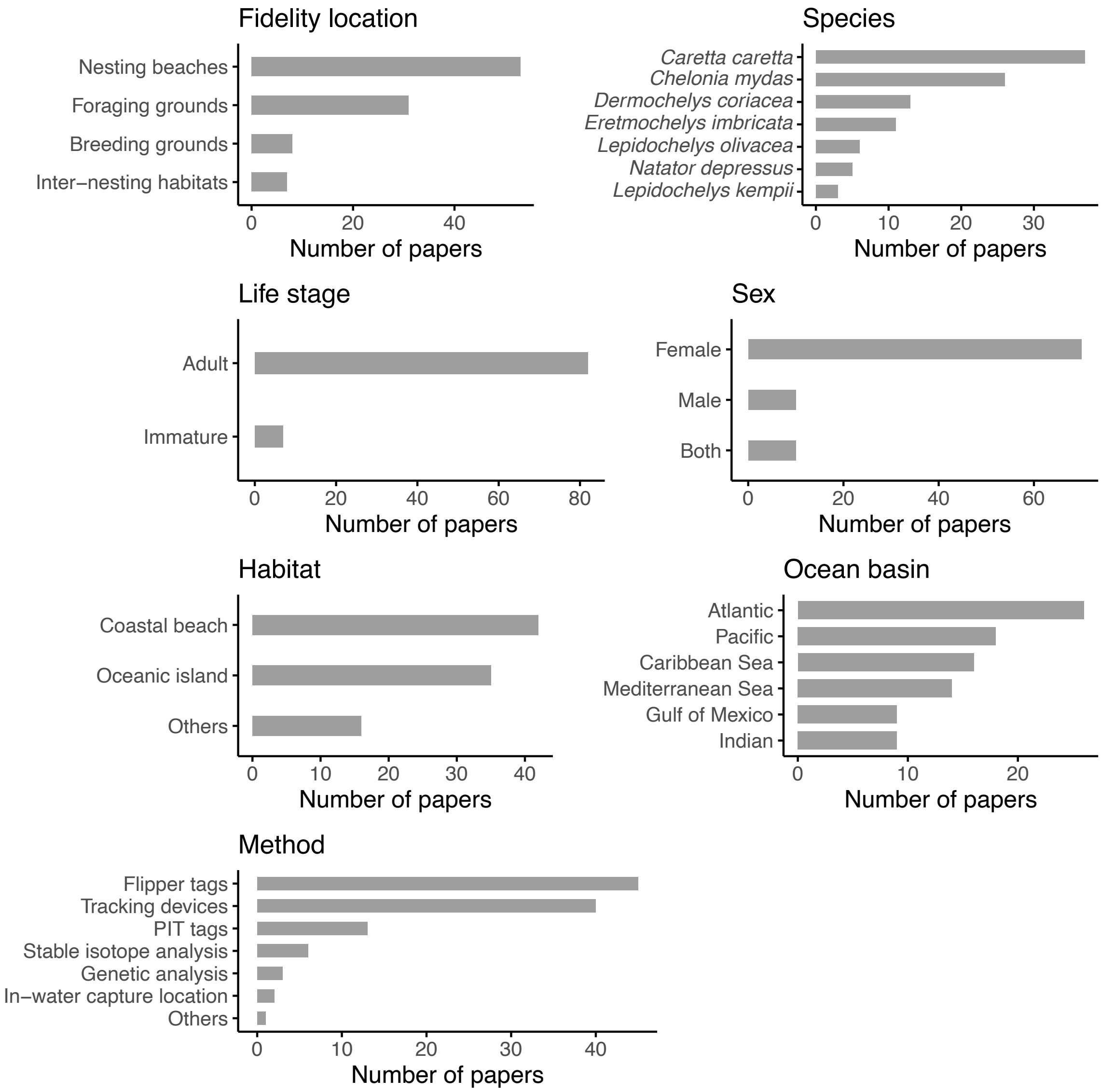

Fig. 5.4. Overview of peer-reviewed papers on sea turtle site fidelity organised by location of site fidelity, species, life stage, sex, habitat, ocean basin and methodology. Except for life stage and sex, the total number of papers per category surpass the total number of papers reviewed (*n* = 89) because some papers provided multiple options for each category

5.4.1. BREEDING SITE FIDELITY

In general, adult female turtles have been found to use the same nesting beach or to use nearby nesting beaches both within a single nesting season and between nesting seasons. Flatback, green, hawksbill *Eretmochelys imbricata*, leatherback *Dermochelys coriacea*, loggerhead, and olive ridley turtles have intra-seasonal records of successful returns to specific nesting beaches (see references in **Table 5.1**). However, these species may exhibit weak site fidelity to their initial nesting beach and shift their nesting locations (**Table 5.1**). In this review, turtles emerging within 5 km on the same beach were considered to display fine-scale site fidelity. This definition encompasses studies where turtles nested within 5 km of their previous nest (e.g., Bannister et al., 2016; Matos et al., 2012) or where the distance between their 2 furthest nesting events (or nesting attempts, if included) was within 5 km (e.g., Barbanti et al., 2022; A. J. B. Santos et al., 2023), and includes those reporting an ultra fine-scale fidelity in the scale of metres (e.g., Hamann et al., 2022; Heredero Saura et al., 2022; Kamel & Mrosovsky, 2005; Patrício et al., 2018). Conversely, turtles that selected different nesting beaches, diverging from their previous chosen nesting beach locations, were classified as exhibiting ‘behavioural plasticity’. All sea turtle species have been observed to faithfully return to a previously visited nesting beach in subsequent years, with inter-annual behavioural plasticity in their site fidelity to the nesting beach described for all of them (see references in **Table 5.2**), except hawksbill and Kemp’s ridley turtles. Remarkably, capture records show that a female loggerhead turtle nested at Mon Repos and nearby beaches in Australia over a 13-year period, from the 1972-1973 to 1985-1986 nesting seasons (Limpus et al., 1992). **Table 5.1** shows the studies that reported site fidelity, fine-scale site fidelity, or plasticity in site fidelity to the nesting beach for each of the 7 sea turtle species during a nesting season. **Table 5.2** provides the same information, but between nesting seasons.

Within and between-seasons fine-scale site fidelity to nesting beaches is documented for flatback, green, loggerhead, and olive ridley turtles (**Table 5.1**, **Table 5.2**), with the flatbacks, greens and loggerheads nesting as close as less than 1 km apart (Bannister et al., 2016; Barbanti et al., 2022; Hamann et al., 2022; Heredero Saura et al., 2022; Limpus et al., 1984; Patino-Martinez et al., 2023; Shimada et al., 2021; Thums et al., 2020). The tendency to return not only to the same nesting beach but also to the same beach section has been previously described both within (e.g., green turtles on Poilão Island, Guinea-Bissau; Patrício et al., 2018; and hawksbill turtles in Guadeloupe, French West Indies; Kamel & Mrosovsky, 2005) and between (e.g., hawksbill turtles in Guadeloupe, French West Indies; Kamel & Mrosovsky, 2006) nesting seasons. Leatherback turtles, a far-ranging species, did not exhibit individual site fidelity at very fine spatial scales, which has been attributed to their larger scale movements (Benson et al., 2011; S. A. Eckert et al., 2006; Morreale et al., 1996). Interestingly, green and olive ridley turtles show different intra and inter-seasonal fine-scale site fidelity patterns (Casale et al., 2023; Heredero Saura et al., 2022). In one study in Costa Rica, green turtle fine-scale site fidelity between seasons was higher, with an average nest distance of 0.14 km, compared to within-season site fidelity, where nests were 0.24 km apart (Heredero Saura et al., 2022). However, this study did not report whether these differences were statistically significant (Heredero Saura et al., 2022). Conversely, Casale et al. (2023) found that olive ridley turtles at Gabon and Congo displayed lower between-season fine-scale site fidelity, with nests averaging 2.1 km apart, compared to within-season site fidelity at 1.7 km, reporting that these differences were not statistically significant.

Table 5.1. Summary of adult female sea turtle within-season site fidelity to the nesting beach by species. Studies in which turtles emerged within 5 km along the same beach were considered as 'fine-scale site fidelity', while those where turtles demonstrated flexibility in their previous chosen nesting beach location were classified as 'behavioural plasticity'. 'NA' denotes no information available

Species	Site fidelity	Fine-scale site fidelity	Behavioural plasticity	References
Caretta caretta	Yes	Yes	Yes	(Bjorndal et al., 1983; Doell et al., 2017; Foley et al., 2013; Godley, Broderick, et al., 2003; K. M. Hart, Lamont, et al., 2013; Hays & Speakman, 1993; Limpus et al., 1992; Marco et al., 2021; Patino-Martinez et al., 2023; Pfaller et al., 2009, 2022; Tucker, 2010; Webster & Cook, 2001)
Chelonia mydas	Yes	Yes	Yes	(Barbanti et al., 2022; Bjorndal et al., 1983; Esteban et al., 2015, 2017; Godley, Lima, et al., 2003; Hamann et al., 2022; Heredero Saura et al., 2022; Limpus et al., 1992; Mortimer & Portier, 1989; Patrício et al., 2018; Read et al., 2014; Shimada et al., 2021; Wang & Cheng, 1999; Xavier et al., 2006)
Dermochelys coriacea	Yes	Yes	Yes	(Benson et al., 2007; Casale et al., 2023; K. L. Eckert et al., 1989; Georges et al., 2007; Horrocks et al., 2016; Kamel & Mrosovsky, 2004; Neeman et al., 2015; Nordmoe et al., 2004; N. Pilcher & Chaloupka, 2013; Santidrián Tomillo et al., 2007; Stewart et al., 2014)
Eretmochelys imbricata	Yes	Yes	Yes	(Esteban et al., 2015; Kamel & Mrosovsky, 2005, 2006; A. J. B. Santos et al., 2023; Soanes et al., 2022; Walcott et al., 2012; Xavier et al., 2006)
Lepidochelys kempii	NA	NA	NA	NA
Lepidochelys olivacea	Yes	Yes	Yes	(Casale et al., 2023; Matos et al., 2012; Tripathy & Pandav, 2008; Whiting et al., 2007)
Natator depressus	Yes	Yes	Yes	(Bannister et al., 2016; Limpus et al., 1984; Thums et al., 2020)

Table 5.2. Summary of adult female sea turtle between-seasons site fidelity to the nesting beach by species. Studies in which turtles emerged within 5 km along the same beach were considered as 'fine-scale site fidelity', while those where turtles demonstrated flexibility in their previous chosen nesting beach location were classified as 'behavioural plasticity'. 'NA' denotes no information available

Species	Site fidelity	Fine-scale site fidelity	Behavioural plasticity	References
Caretta caretta	Yes	Yes	Yes	(Bjorndal et al., 1983; Foley et al., 2013; K. M. Hart, Lamont, et al., 2013; Hays & Sutherland, 1991; Limpus et al., 1992; Limpus & Limpus, 2001; Patino-Martinez et al., 2023; Pfaller et al., 2009; Phillips et al., 2021)
Chelonia mydas	Yes	Yes	Yes	(Barbanti et al., 2022; Godley, Lima, et al., 2003; Heredero Saura et al., 2022)
Dermochelys coriacea	Yes	NA	Yes	(Casale et al., 2023; Hilterman & Goverse, 2007; Horrocks et al., 2016; N. Pilcher & Chaloupka, 2013; Santidrián Tomillo et al., 2007; Stewart et al., 2014)
Eretmochelys imbricata	Yes	Yes	NA	(Kamel & Mrosovsky, 2006; Levasseur et al., 2021; A. J. B. Santos et al., 2023; Walcott et al., 2012)
Lepidochelys kempii	Yes	NA	NA	(Gredzens & Shaver, 2020)
Lepidochelys olivacea	Yes	Yes	Yes	(Casale et al., 2023; Tripathy & Pandav, 2008; Whiting et al., 2007)
Natator depressus	Yes	Yes	Yes	(Limpus et al., 1984; Thums et al., 2020)

Another study found that olive ridley turtles in Brazil tended to lay consecutive clutches closer to each other as the nesting season progressed (Matos et al., 2012). Exclusive within-season fine-scale site fidelity to nesting beaches was observed for leatherback turtles (**Table 5.1**), with average nest distances of 3.2 or 4.1 km in Gabon and Congo, and Costa Rica, respectively (Casale et al., 2023; Neeman et al., 2015). Large scale displacements are well described for loggerhead turtles, with average distances of 27.5 km (and a maximum displacement of 402.1 km) between emergences in the Northern Gulf of Mexico (K. M. Hart, Lamont, et al., 2013) and 25.8 km (maximum displacement of 109.1 km) between their most distant nests in Florida, USA (Tucker, 2010). Similarly, leatherback turtles exhibit large scale displacements, with an average distance of 25.1 km (maximum displacement of 491.6 km) between nests across nesting seasons in Gabon and Congo (Casale et al., 2023).

Adult female turtles can return to the same in-water site throughout the breeding season (i.e., their inter-nesting habitat). This pattern has been observed in green (Raposo et al., 2023; Shimada et al., 2021), hawksbill (A. J. B. Santos et al., 2023), and loggerhead turtles (Marcovaldi et al., 2010), with green turtles displaying up to 5 inter-nesting overlapping areas (Raposo et al., 2023). Hawksbill (A. J. B. Santos et al., 2023) and loggerhead turtles (Phillips et al., 2021) have demonstrated site fidelity to inter-nesting habitats in subsequent years, as well as flexibility in this behaviour, i.e., not returning to a previously established inter-nesting site (Hawkes et al., 2012; Mingozzi et al., 2016; Phillips et al., 2021).

Male site fidelity to breeding grounds has been mostly inferred through tracking (James et al., 2005; Schofield et al., 2020; Van Dam et al., 2008; Varo-Cruz et al., 2013) and tagging (Grossman et al., 2019; Limpus, 1993; Pandav et al., 2000) methodologies, although molecular-based paternity analysis has also been used (Wright et al., 2012). Adult male site fidelity to breeding grounds has been reported to a lesser extent in green (Grossman et al., 2019; Limpus, 1993; Wright et al., 2012), hawksbill (Van Dam et al., 2008), leatherback (James et al., 2005), loggerhead (Schofield et al., 2020; Varo-Cruz et al., 2013) and olive ridley turtles (Pandav et al., 2000).

5.4.2. FORAGING SITE FIDELITY

Foraging site fidelity has been observed in immature and adult sea turtles, including both sexes. Limited data suggests that immature turtles exhibit fidelity to preferred sites, with turtles returning to specific sites after intentional displacements ranging from at least 1 to 20 km during the year they were displaced or in subsequent years (Avens et al., 2003; N. Pilcher, 2010; Rudloe & Rudloe, 2005), or following seasonal movements (A. T. Coleman et al., 2017; González Carman et al., 2016; Snape et al., 2020), particularly in loggerhead and Kemp's ridley turtles. Displacement studies have shown foraging site fidelity in green (N. Pilcher, 2010), loggerhead (Avens et al., 2003) and Kemp's ridley turtles (Rudloe & Rudloe, 2005). For example, an immature Kemp's ridley turtle released 6.4 km from its capture location returned to its initial site (Rudloe & Rudloe, 2005). However, immature green turtles also exhibit foraging site plasticity (J. M. Blumenthal et al., 2010). An immature green turtle was found in a new site more than 2 years after its initial capture (J. M. Blumenthal et al., 2010).

Similarly, adult sea turtles (both males and females) can return to their previously visited foraging sites or relocate to alternative locations (see references in **Table 5.3**). Female loggerhead turtles have been observed to return to their previously visited foraging sites after long-distance breeding migrations of up to 2400 km, with remigration intervals (the number of years between successive reproductive seasons) of 2 or 3 years (Marcovaldi et al., 2010). Male loggerhead turtles have also been recorded returning to the same foraging sites, after migrating to breeding grounds or exploring new areas, with distances between sites of more than 25 km and with periods ranging from 52.2 to 361.2 d (Dujon et al., 2018). At the species level, flatback, green, hawksbill, Kemp's ridley and loggerhead turtles exhibit foraging site fidelity, but greens, Kemp's ridleys and loggerheads were also shown to exhibit shifts in their feeding locations (**Table 5.3**). It is worth noting that most research has focused on green and loggerhead turtles. In terms of life stages, foraging site fidelity and plasticity has been recorded for both males and females (**Table 5.3**). There is also evidence of long-term foraging site fidelity. For instance, a female green turtle was recaptured at the same feeding location 12 years after being originally flipper-tagged (Read et al., 2014). A particularity of this behaviour is that females may bypass other known foraging sites as they make their return journey from breeding migrations (A. C. Broderick et al., 2007; Shimada et al., 2020), and once on the foraging grounds, they may shuttle between nearby sub-areas while remaining faithful to both (Haywood et al., 2020; Mingozzi et al., 2016). **Table 5.3** presents the studies that investigated foraging site fidelity or plasticity in site fidelity to foraging grounds for each sex of the 7 sea turtle species.

Table 5.3. Summary of adult sea turtle foraging site fidelity by species and sex. Studies in which turtles demonstrated flexibility in their previous chosen feeding location were classified as 'behavioural plasticity'. 'NA' denotes no information available

Species	Sex	Site fidelity	Behavioural plasticity	References
Caretta caretta	Female	Yes	Yes	(A. C. Broderick et al., 2007; Ceriani et al., 2023; Dujon et al., 2018; D. R. Evans et al., 2019; Fujita et al., 2023; Hatase et al., 2013; Haywood et al., 2020; Limpus et al., 1992; Limpus & Limpus, 2001; Marcovaldi et al., 2010; Mingozzi et al., 2016; Phillips et al., 2021; Shimada et al., 2020; Tucker et al., 2014; H. B. Vander Zanden et al., 2014)
	Male	Yes	Yes	(Casale et al., 2013; Dujon et al., 2018; Schofield, Hobson, Fossette, et al., 2010; Shimada et al., 2020; Thomson et al., 2012)
Chelonia mydas	Female	Yes	Yes	(J. Blumenthal et al., 2006; Bradshaw et al., 2017; A. C. Broderick et al., 2007; Limpus et al., 1992; N. J. Pilcher et al., 2021; Read et al., 2014; Shimada et al., 2020; K. L. Stokes et al., 2015)
	Male	Yes	NA	(N. J. Pilcher et al., 2021; Shimada et al., 2020)
Dermochelys coriacea	Female	NA	NA	NA
	Male	NA	NA	NA
Eretmochelys imbricata	Female	Yes	NA	(Hawkes et al., 2012; Shimada et al., 2020)
	Male	NA	NA	NA
Lepidochelys kempii	Female	Yes	Yes	(Gredzens & Shaver, 2020)
	Male	NA	NA	NA
Lepidochelys olivacea	Female	NA	NA	NA
	Male	NA	NA	NA
Natator depressus	Female	Yes	NA	(Shimada et al., 2020)
	Male	NA	NA	NA

5.5. GENERAL LEARNINGS ON SEA TURTLE SITE FIDELITY

Returning to the same nesting beach is a common trait of adult female sea turtles, and this behaviour can persist for more than a decade (e.g., Limpus et al., 1992). However, variation in egg-laying sites does occur and is a shared pattern across species. Still, I caution that there has been less research on flatback, Kemp’s ridley and olive ridley turtles than on other sea turtle species, which may constrain general conclusions. Green and hawksbill turtles exhibit a general trend of site fidelity to nesting beaches, with the former also being faithful to inter-nesting habitats. On the other hand, leatherback and loggerhead turtles appear to be more flexible when repeating their nesting and inter-nesting habitats. Sea turtles provide no parental care after oviposition, thus environmental conditions during incubation influence hatching success, hatchling physical characteristics (Patrício et al., 2018), and sex ratios (Mrosovsky, 1994; Mrosovsky & Provancha, 1989; Mrosovsky & Yntema, 1980). Plasticity in this behaviour allows the colonisation of new nesting sites, possibly driven by local beach dynamics. For example, leatherback turtles that had nested at Kolukumbo beach in Suriname prior to 2004 shifted to a different location after the beach became unsuitable (Hilterman & Goverse, 2007). For site-faithful species, several theories have been proposed to explain fine-scale nesting beach selection, including (i) its dependence on environmental conditions (Santidrián Tomillo et al., 2007) and (ii) the heritability of returning to a specific nesting site (Kamel & Mrosovsky, 2005), though the latter still requires further clarification in sea turtles (Patrício et al., 2018). Site fidelity during successive inter-nesting intervals can help conserve energy for egg development, travel to and from the nesting beach and egg-laying. In contrast, even when food is available, exploratory forays away from the usual areas may help restore female energy reserves through foraging during this period (Hays, Glen, et al., 2002; Myers & Hays, 2006). Male turtles site fidelity to breeding grounds is overall understudied. Nevertheless, one study reported recaptures of 8 males up to 10 years after their initial capture at their mating area (Grossman et al., 2019), suggesting long-term breeding site fidelity comparable to females.

A common pattern in foraging site fidelity among sea turtle species is difficult to discern because most research has focused on green and loggerhead turtles. This constrains our ability to identify broader trends across all species. The limited number of studies on immature and adult male turtles further challenges broad generalisations even at the species level. However, both life stages and sexes exhibit foraging site fidelity, with females showing long-term site fidelity for over a decade (Read et al., 2014). Currently, the selection of foraging grounds by sea turtles is commonly explained by the hatchling drift hypothesis, wherein oceanic currents that drive hatchling dispersal may influence where individuals forage as adults (Hays et al., 2010). It is also postulated that turtles retain fidelity to the foraging grounds that they first encountered as hatchlings or juveniles, possibly due to geomagnetic imprinting (Lohmann, Putman, et al., 2008). Consecutively using a known foraging ground is advantageous as turtles have information about food quality and reliability (Shimada et al., 2020). Given the risks of moving to unknown areas, passing through other potential foraging grounds to remain faithful to familiar ones does not appear unusual (Shimada et al., 2020). The particularity of females remaining faithful to neighbouring foraging grounds is most likely due to seasonal fluctuations in foraging opportunities and/or specific environmental conditions unique to each site (Mingozzi et al., 2016).

5.6. KNOWLEDGE GAPS

Despite the increasing research on sea turtle site fidelity over the last 20 years, several knowledge gaps still exist. To date, most studies have concentrated on the terrestrial habitat, likely because researchers have easier access to female turtles on the nesting beach (Godley et al., 2008). As a result, there is limited understanding of site fidelity beyond nesting beaches, such as the repeated use of inter-nesting habitats and breeding grounds by females and males, respectively. For example, there are few studies examining inter-nesting intervals alongside site fidelity. Compared to the terrestrial life history phase, sea turtles' faithfulness to foraging grounds remains poorly understood. Additionally, research has predominantly focused on nesting females, while studies on immature and adult male turtles are lacking. The movements and spatial distribution of these groups continue to be largely unknown (Hays & Hawkes, 2018). Another gap in assessing sea turtle site fidelity is the uneven geographic distribution of studies. Although research on site fidelity has been conducted in various regions of the world, it is not evenly distributed. The majority of studies are concentrated in North America, while Africa and Oceania are comparably data deficient regions. Moreover, despite all 7 sea turtle species being able to return to previously visited areas, this behaviour has not been systematically studied for all species. In particular, flatback, Kemp's ridley and olive ridley turtles are the least studied.

5.7. CHALLENGES AND STRATEGIES

One major challenge regarding sea turtle site fidelity research is linked with biases in tagging programs, including biases in tag recaptures and biases in tag returns. Biases in tag recaptures occur because of tag loss (Casale et al., 2023) or insufficient beach coverage (Mortimer & Portier, 1989; Shamblin et al., 2021). These are often related to funding and logistical limitations, but also to difficulty of accessing remote sites, resulting in differences between sampling and nesting areas. Several studies have estimated tag loss in sea turtles (e.g., Bjorndal et al., 1996; Casale et al., 2023; Limpus, 1992; Nishizawa et al., 2018; Pfaller et al., 2019; Rivalan et al., 2005) with some describing a high initial loss followed by a constant loss rate over time (Casale et al., 2023; Nishizawa et al., 2018; Pfaller et al., 2019; Rivalan et al., 2005). The rate of tag loss is expected to have a smaller influence on the estimation of site fidelity in a single nesting season (within-season site fidelity to the nesting beach and inter-nesting site fidelity) than on the estimation of site fidelity across years (between-season site fidelity to the nesting beach). One way to overcome tag loss might be to use both flipper and PIT tags, as the latter are generally more durable and resistant to loss (Omeyer et al., 2019). In addition, challenges hindering tag returns (i.e., the low probability of reporting resighted flipper tags) result from illegal harvesting, since tagged turtles that are illegally caught tend to be less reported (Horrocks et al., 2011). These biases could be mitigated by encouraging people to report any flipper-tagged turtles that are caught (Troëng & Chaloupka, 2007), whether as bycatch or through poaching.

Another key challenge in sea turtle site fidelity research is connected with tracking methodologies. Such challenges involve short tracking durations (e.g., Shimada et al., 2021), and small sample sizes (e.g., Esteban et al., 2015), most likely associated with the failure or loss of tracking devices (Whiting et al., 2007) and their high cost. Understandably, those studies with short tracking durations should be interpreted with caution since they may reflect the limitations of the tracking period and thus longer periods could have provided different outcomes (Tucker et al., 1995). Remarkably, some previous research reported tracking durations of up to approximately 1280 (Marcovaldi et al., 2010) and 1500 d (Mingozzi et al., 2016), which have allowed the recording of movements between at least 2 reproductive seasons. Several recommendations have been proposed to enhance the design of tracking devices used in sea turtle research. These include refining the profile and attachment location of the devices to reduce hydrodynamic drag, exploring alternative energy sources to extend tracking duration, and optimising antenna design and material to increase durability and transmission quality (Piacenza et al., 2018). Despite the fact that SIA can only be used to suggest foraging site fidelity and cannot address other types of site fidelity, the issue of small sample sizes for foraging site fidelity studies can be tackled by combining satellite tracking of a few individuals with SIA of those individuals alongside a larger sample (Haywood et al., 2020).

Sea turtle site fidelity research is also geographically biased, with more studies conducted in regions with larger economies compared to developing regions with limited research funding. Consequently, there is an unequal distribution of research efforts across species and regions. In fact, a previous study on global trends in sea turtle research over the last 3 decades found that a large amount of research efforts are motivated by funding and logistical availability, in addition to local conservation needs and specific research interests (N. J. Robinson et al., 2023).

Overall, fidelity is frequently assessed through traditional tagging or tracking methodologies. However, previous research has demonstrated that using both tagging and tracking may provide distinct results in terms of site fidelity vs. plasticity. For instance, while tracking revealed fidelity, flipper tagging highlighted plasticity (Esteban et al., 2015; Raposo et al., 2023). Tracking often focuses on detailed information (e.g., routes) over limited periods due to the battery life or failure of tracking devices and thus frequently emphasizes fidelity, particularly with shorter recording durations. In contrast, flipper tagging tends to reveal broader behavioural patterns over longer periods, considering that tags remain in place, hence capturing plastic behaviour on a larger scale. Therefore, combining complementary approaches may be the most effective strategy to overcome the individual limitations of each methodology and gain a better understanding of sea turtle site fidelity and plasticity.

Complementary approaches, such as male paternity studies that provide indirect evidence of site fidelity to specific rookeries (Wright et al., 2012) or molecular genetic studies targeting female turtles that allow to identify fidelity patterns (Levasseur et al., 2021; Pfaller et al., 2022), can also shed light on site fidelity. However, these methodologies have only been used more recently and in fewer studies compared to those using tagging and tracking.

On top of the aforementioned challenges, contextualising site fidelity remains difficult due to a lack of clarity in definitions in the literature. A useful approach would be to standardize the concept of site fidelity, which can be accomplished by using the definition presented in this review. This definition, which refers to returning to a previously visited breeding or foraging area and has been used in other studies (e.g., Esteban et al., 2015; Nordmoe et al., 2004), distinguishes this study from others that have focused on residency (e.g., Naro-Maciel et al., 2018; Nivière et al., 2018; Tanabe, Cochran, Williams, et al., 2023), or even those examining natal philopatry (e.g., Allard et al., 1994; Bowen et al., 2005; Meylan et al., 1990).

5.8. FUTURE RESEARCH PRIORITIES

Understanding sea turtle site fidelity is essential for effective conservation planning because it helps to identify key conservation areas that turtles return to and consequently guide management efforts. Sea turtles are exposed to natural and anthropogenic threats throughout their life cycle. For example, they are vulnerable to predation and habitat loss or alteration due to sea level rise, coastal erosion, and development on nesting beaches during the nesting, incubation and hatching phases (Fuentes et al., 2023). At sea, they are at risk from fisheries interactions (Donlan et al., 2010; Fuentes et al., 2023), pollution (Barraza et al., 2020; Cortés-Gómez et al., 2017; Kühn & van Franeker, 2020; Villa et al., 2017), degradation of foraging habitats (López-Mendilaharsu et al., 2020), among others. Inter-nesting habitats concentrate adult female turtles, which can become vulnerable to anthropogenic threats (Whiting et al., 2007; Zbinden et al., 2007). Similarly, turtles are also susceptible to human-related activities in foraging grounds (K. M. Hart et al., 2018), while adult male turtles at breeding grounds face the risk of exploitation (P. T. Plotkin et al., 1996). A sound definition of protected areas and periods of protection could thus contribute to the effective conservation of these animals during this vulnerable period. However, there are still major uncertainties about the extent of site fidelity during these periods. Therefore, expanding the overall knowledge of site fidelity to inter-nesting habitats, breeding and foraging grounds is essential for guiding targeted conservation actions to protect the repeatedly visited areas. Additionally, determining overlaps between turtle habitat use and anthropogenic threats should be regarded as a priority (Coll et al., 2012; A. J. B. Santos et al., 2021; Schofield et al., 2013; K. L. Stokes et al., 2015; Troëng et al., 2004). For example, site fidelity during the inter-nesting period can reduce the risk of anthropogenic interactions, while a wandering behaviour may increase exposure to fisheries (e.g., A. J. B. Santos et al., 2021; Tucker et al., 1995; Whiting et al., 2007). Detailed (fine-scale) spatial data on sea turtle site fidelity, particularly during nesting, can also help detect patterns that heighten risks. This data can inform management strategies to mitigate both natural and human-induced threats. Furthermore, understanding sea turtle site fidelity can help determine which individuals will be most affected by climate change and guide adaptive conservation, such as protecting heavily used areas from rising sea levels and temperatures.

On the non-fidelity side, turtles with pronounced plastic behaviour, who may breed or forage across extensive areas, may become particularly vulnerable to threats across multiple jurisdictions, making international cooperation critical for their effective protection (J. Blumenthal et al., 2006; Horrocks et al., 2016; Maxwell et al., 2011; Meylan, 1999; Resendiz et al., 1998). Hence, resolving site fidelity patterns is fundamental to facilitate cross-border cooperation and develop multinational conservation strategies.

Immature and adult male turtles are essential for population viability (Hays et al., 2022; Wildermann et al., 2018). Nevertheless, both these life stages have only restricted in-water accessibility to researchers, limiting research progress in comparison to female turtles. Given the lack of data on these life stages, another research priority is to increase our understanding of their site fidelity. Capturing immature or adult male turtles can be operationally challenging and costly, thus photo-identification methods may be a useful alternative (Schofield et al., 2008). Additionally, there is the need to allocate more research efforts to specific geographic regions, like Africa and Oceania, and understudied sea turtle species, like flatback, Kemp's ridley and olive ridley turtles. A critical factor that may contribute for the geographic and species level biases is the global discrepancy in how conservation funding is allocated across different regions (Halpern et al., 2006).

So far, heritability of site selection remains largely unresolved. It has been proposed for nesting beaches but with the caveat that additional studies are required (Patrício et al., 2018), while during foraging it has been mentioned as a potential research interest (H. B. Vander Zanden et al., 2014). Therefore, clarifying if fidelity to nesting and foraging sites are heritable traits should be a future research focus in sea turtle science.

5.9. FINAL REMARKS

Site fidelity can facilitate targeted conservation efforts as conservation programs can focus on known breeding and foraging high-use areas. This focused conservation actions allow better use of available financial and logistical resources. Conservationists can use site fidelity data to help protect critical habitats like nesting beaches from natural or anthropogenic threats. Furthermore, knowledge on breeding and foraging hotspots allows to study specific populations over time.

Sea turtle site fidelity information can be challenging to collect from the literature due to ambiguous definitions or because site fidelity is often inferred from studies focused on other topics. In addition to using the definition of site fidelity provided in this review, studies that primarily focus on other topics but also address this issue should include 'fidelity' as a keyword to facilitate and improve the efficiency of the search process. Ultimately, addressing the knowledge gaps and research priorities set in this review will enhance our understanding of sea turtle site fidelity at the species level, across different life stages and sexes, and in various geographic regions globally. Since some studies have shown that employing different methodologies (namely tagging vs. tracking) may provide contrasting results regarding site fidelity vs. plasticity, I recommend using multiple methodologies, whenever possible, to better infer site fidelity.

CHAPTER 6

GENERAL DISCUSSION


Cheila Raposo

GENERAL DISCUSSION

The study of spatial distribution and nesting dynamics is essential for the effective protection of sea turtles (Willson et al., 2020; Zbinden et al., 2007). This PhD thesis has enhanced our understanding of these topics in the green turtle *Chelonia mydas* population that reproduces in the João Vieira-Poilão Marine National Park (hereafter 'JVPMNP') and has contributed with baseline knowledge that can be applied to support its conservation by: (i) investigating the inter-nesting movements of breeding females to determine their spatial distribution, site fidelity, and inter-island linkages within the JVPMNP (Chapter 2), (ii) evaluating datasets on clutch survival and associated threats at Poilão, and 3 neighbouring islands within the JVPMNP (Chapter 3), (iii) examining the nutrient input from green turtle eggs and hatchlings into the coastal communities of the JVPMNP (Chapter 4), and (iv) compiling a comprehensive overview of current information on sea turtle site fidelity (Chapter 5).

The first original research chapter (Chapter 2) of this thesis aimed to investigate the fine-scale movements of female green turtles during the breeding period within the JVPMNP. This is a key step to design effective management and protection strategies, such as identifying areas of conservation priority (e.g., T. M. Dawson et al., 2017; K. M. Hart et al., 2019; Schofield, Hobson, Lilley, et al., 2010). It is particularly relevant in light of potential overlaps between turtle habitat use and anthropogenic threats. We showed that Poilão's breeding green turtles remained within a restricted area around Poilão Island during their inter-nesting intervals, with approximately half of their home range falling within an area fully protected from fishing and other human impacts within the JVPMNP marine protected area (MPA). However, female turtles likely spent just as much time within a peripheral area, partially protected, where fishing is allowed to local residents and licensed recreational fishers using regulated equipment, facing the risk of fisheries interactions, namely bycatch and targeted fishing by artisanal fishing vessels (Allman et al., 2021; J. L. D. dos Santos et al., 2024) and, potentially, vessel strikes (Fuentes et al., 2021; Shimada et al., 2017). This thesis highlights the importance of ensuring that at-sea patrolling is conducted effectively within this MPA, as illegal fishing persists within the JVPMNP, including in the central no-take zone. Furthermore, it emphasizes the need for flexible conservation actions at the local level. A positive outcome of this thesis would be the adoption by JVPMNP decision-makers of a temporal extension of the no-take zone (e.g., A. J. B. Santos et al., 2021; Schofield et al., 2013; A. C. C. D. Silva et al., 2010; Witt et al., 2008), coincident with the green turtle peak breeding season (from August to September), to encompass the area westwards of Poilão. This could reduce the overlap between turtle habitats and fishing activities, and thus enhance the protection of turtles during the critical breeding period. Additionally, we showed that female turtles tended to exhibit fidelity to inter-nesting sites, which is probably a strategy to save energy. Experienced breeders may further potentially benefit from energy saving by moving less and occupying smaller areas over time. This research provide evidence that biases may occur in future tracking studies that only use turtles tagged later in the nesting season. Tagging turtles towards the end of the nesting season may mostly capture data from experienced breeders who move less, which can mislead the interpretation of habitat use and influence management decisions.

The Chapter 3 of this thesis focused on evaluating the potential of Poilão's neighbouring islands as alternative nesting sites if conditions at Poilão deteriorate due to density-dependent factors, whether linked to climate change (i.e., global mean sea level rise and reduction of the available nesting area) or to green turtle population growth. Our assessment of clutch survival and associated threats (predation and flooding) on Poilão and its 3 satellite islands (Cavalos, Meio and João Vieira) revealed that clutch predation and flooding were higher on Poilão's neighbouring islands. This finding can potentially influence the implementation of conservation actions to mitigate the effects of predation and flooding on turtle nests, as already happens on other regions (Z. P. Butler et al., 2020; Chacón-Chaverri & Eckert, 2007; Liles et al., 2019; Lovemore et al., 2020; S. Martins et al., 2022; Nordberg et al., 2019; O'Connor et al., 2017; Sampaio et al., 2022). Namely, our findings suggested the presence of a source-sink dynamic within this 4-island system, as evidenced by clutch predation and flooding patterns, along with the linkages established by female turtles between JVPMNP islands. In this perspective, migrants from the source habitat (Poilão), which currently offers the best conditions for clutch survival, use the low reproductive output sink habitats (the neighbouring islands). This chapter may serve as a guide for JVPMNP decision-makers, providing a basis for carefully evaluating the costs and benefits of conservation efforts targeting the sink habitats, considering their limited contribution to the long-term sustainability of the green turtle population in the JVPMNP. Prioritizing the preservation of the source habitat may provide a worthier long-term advantage, but monitoring the sink habitats and maintaining minimal conservation efforts may still be useful to ensure population resilience, for instance, if the current source habitat becomes severely compromised.

In Chapter 4, we evaluated the potential nutrient contribution by green turtles to coastal communities of the JVPMNP, and we showed that green turtles are an important nutrient source to the coastal ecosystem of Poilão. In this island, the plant community is influenced by its proximity to the shoreline and the availability of nutrients derived from sea turtle nests, with shoreline plants assimilating a ^{15}N source, likely from green turtle eggs. Similarly, ghost crabs and sea catfishes rely on green turtle eggs and hatchlings, with this being a localised trend that does not extend inland or into offshore areas. Green turtles on Poilão Island may assist in the maintenance of the shoreline by crossing the ocean-land boundary and supplying nutrients to plants, promoting their growth (Moss, 2017). Consequently, they help to preserve this habitat, which is also essential for their reproductive success. Furthermore, green turtles provide a direct nutrient source to terrestrial and marine predators in Poilão, probably influencing community dynamics. Specifically, the high abundance of green turtle eggs and hatchlings around the end of the breeding season temporarily shifts ghost crabs' diet, causing these animals to extensively rely on them. This can potentially alter the interactions between ghost crabs and other prey species. It is known that predators can adapt their diet by shifting to alternative prey types when the abundance of their primary prey declines, allowing them to meet the nutritional needs that the primary prey previously provided and supporting the recovery of the primary prey population (Brunet et al., 2023). Reasonably, seasonal increases in localised prey can also be beneficial in terms of nutritional needs, leading to changes in predator foraging behaviour at the JVPMNP. Besides, sea catfishes may concentrate their activity around Poilão Island during the green turtle breeding season to exploit this abundant food source. In both cases, the nutrient input from green turtle clutches to terrestrial habitats and its subsequent use by predators, whether terrestrial or marine, as nutrients return to the sea in the form of hatchlings or eroded and unhatched yet intact eggs that are washed out (Chapter 4 of this thesis; Avenant et al., 2024; Bouchard & Bjorndal, 2000), promote nutrient cycling and energy fluxes (Avenant et al., 2024), influencing the productivity of the Poilão ecosystem. Moreover, the nutrient input along the beaches of Poilão may influence meiofaunal communities (Diane et al., 2017), although we did not focus on this potential ecological role. By exemplifying the ecological roles of green turtles in Poilão, we also underscored the importance of this species to the local ecosystem.

The final original research chapter (Chapter 5) of this thesis presented the first review of the literature on sea turtle site fidelity, including (i) female site fidelity to nesting beaches and to (ii) inter-nesting habitats, (iii) male site fidelity to breeding grounds, and (iv) fidelity to foraging grounds (both sexes). Site fidelity is considered here as the return to previously visited areas. Despite decades of research focusing on behaviour and movement patterns of breeding and foraging sea turtles, this is the only detailed review of sea turtle site fidelity studies thus far. Therefore, Chapter 5 provides a timely work, suitable to guide future sea turtle research. In general, this chapter revealed that some sea turtle species tend to exhibit fine-scale fidelity, even though all species are site-faithful. Similarly, plasticity is a shared trait among all species. Site fidelity is observed in both female and male turtles, including site fidelity to foraging grounds. Importantly, Chapter 5 underscores the need for a standardized concept of site fidelity that should be used in future studies to congregate sea turtle site fidelity research and avoid ambiguity.

6.1. FUTURE RESEARCH

Assessing the effectiveness of MPAs to support populations of species of conservation concern is essential to ensure that these species receive adequate protection (A. J. B. Santos et al., 2021). This is highly important in areas used by breeding female turtles, since they have been attributed the highest reproductive value (i.e., their potential to contribute offspring to future generations; Bolten et al., 2011) within a population. By combining the information on green turtle spatial distribution at the JVPMNP provided in this thesis with future data on exposure to fisheries threats – an important line of investigation – it is possible to better comprehend whether the existing MPA provides adequate support for Poilão's breeding green turtle population. For example, a previous study combined satellite tracking, fishing effort, and bycatch data to identify areas of higher vulnerability to sea turtles in the Hawaii-based swordfish fishery (Howell et al., 2015). This multi-approach analysis subsequently identified areas with specific sea surface temperatures associated with high turtle occurrence, which served as a proxy for turtle habitat, providing a dynamic management guidance to fishers to reduce bycatch (Howell et al., 2015). On the other hand, although adult male turtles may not hold as much reproductive value as females, they may become more important to ensure long-term population sustainability as hatchling sex ratios become increasingly female-biased due to rising incubation temperatures (Hays et al., 2022). Thus far, information about adult male turtles in the JVPMNP is scarce, with one study revealing that most males remain near Poilão Island during the peak breeding season (Beal et al., 2022). Therefore, expanding the overall knowledge of the spatial distribution of male green turtles may be locally important in the face of potential threats and in the context of a warming climate.

The green turtles that nest at the JVPMNP are thought to forage within the Bijagós Archipelago but also in international waters, in The Gambia, Senegal and Mauritania (Godley et al., 2010; Patrício et al., 2022). Further decoding foraging grounds is thus crucial to inform marine spatial planning, especially if these areas overlap with a certain threat, such as bycatch or alteration of the marine habitat (López-Mendilaharsu et al., 2020).

Climate-related threats (sea level rise, SLR, and coastal erosion) will reduce the current available green turtle nesting areas across JVPMNP islands. In addition, findings from this thesis indicate that Cavalos, Meio and João Vieira have limited potential to support the reproduction of sea turtles. Understanding how JVPMNP beaches will be impacted by SLR is thus essential to prioritize conservation efforts and adopt viable mitigation strategies, such as those suggested in Chapter 3 (e.g., relocating turtle eggs at risk of flooding to safer areas in the same beach).

Information on the number of nests per year can be used as a proxy for assessing long-term nesting population abundance trends, reflecting variability in nesting abundance and reproductive output over time (Restrepo et al., 2023). Like previous work (Broderick & Patrício, 2019; Patrício et al., 2019), this thesis highlighted that the number of green turtle nests per year in Poilão is increasing, although with high inter-annual variation. This suggests that the ongoing annual sea turtle monitoring campaigns in Poilão since the year 2000 have been effective for the long-term protection of this population of green turtles. Continued monitoring should remain a priority for the management of the JVPMNP since it is important to verify the success of conservation efforts.

This thesis provides the first assessment of how green turtle eggs and hatchlings contribute nutrients to the nutrient-poor sandy beach ecosystem and the adjacent nearshore environment in Poilão. Based on this background, future research endeavours could focus on: (i) repeat the methodology used in Chapter 4 of this thesis in years with higher number of nests, since 2021 and 2022 had a low number of nests registered in Poilão (IBAP, unpub. data), resulting in a potentially reduced availability of nutrients to primary producers and predators; (ii) compare the nutrient input by the end of the green turtle breeding season (October/November) with that approximately 4 months later (around February/March), to cover the full incorporation of the isotopic signal of turtle egg or hatchling nutrients into consumer tissues; and (iii) assess green turtle nutrient input across a spatial gradient within Poilão Island, by collecting vegetation samples along transect lines extending from the water line up to 50 m into the forest (Bai et al., 2009). On the other hand, it would be important to investigate nutrient cycling and its impact on the local ecosystem. Since some of the nutrients from sea turtle nesting activities on beaches return to the sea as hatchlings (Avenant et al., 2024; Bouchard & Bjorndal, 2000), it would be important to quantify both the percentage of green turtle nest-derived nutrients that remain in the beach ecosystem and the amount that is transported seaward as hatchlings. Similarly, the effect of nutrient input from green turtle clutches on predator fitness was not evaluated, but it is recognised that nutritional enrichment can lead to higher biomass production (Cross et al., 2006; Polis et al., 1997).

The review on sea turtle site fidelity presented in Chapter 5 of this thesis allowed the identification of common patterns, such as the fact that most research has focused on site fidelity to the nesting beach. However, it also identified knowledge gaps and challenges in understanding site fidelity in sea turtles, as well as several potential future research opportunities. For example, a need for better understanding of site fidelity at inter-nesting habitats, breeding and foraging grounds, as well as for the determination of overlaps between turtle habitat use and anthropogenic threats. Addressing the research priorities presented in Chapter 5 will enhance our understanding of sea turtle site fidelity at the species level, across different life stages and sexes, and in various geographic regions worldwide, contributing to their conservation.

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APPENDIX: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 2

Protocol S2.1. Deployment of tracking devices on adult female green turtles in Poilão Island, Bijagós Archipelago, Guinea-Bissau

We deployed the tracking devices during the egg-laying process. We waited at a safe distance for female turtles to start laying eggs, and then approached to attach the tags. Handling time was reduced to the strictly necessary to minimize disturbance to the turtles and all females maintained their nesting activity during and after tag deployment and returned safely to the sea. The second anterior central carapace scute of each turtle was sanded with sandpaper and degreased with acetone, before being fitted with a fixative made of fiberglass and fast-dry epoxy (Devcon 5 Minute® Epoxy). This fixative was left to dry for 5 min. Then, a layer of two-part steel resin (magic metal, ®Loctite) was applied at the base of the tag, which was then centred in the fixative, and left to dry for 10 min. Lastly, more fixative was applied around the base of the tag to secure it and left to dry for 5 min. The tracking device attachment procedure took approximately 20 min.

The protocols were approved by the ethical committee of the Órgão Responsável pelo Bem-Estar Animal of Ispa – Instituto Universitário, Lisbon, Portugal (ORBEA-Ispa), which ensures the compliance of ethical standards and animal welfare rules.

Green turtle with Wildlife Computers ® SPOT-375B tag

Table S2.1. Summary information from 44 female green turtles tracked during the 2018, 2019 and 2020 breeding periods within the João Vieira-Poilão Marine National Park (JVPMNP), Bijagós Archipelago, Guinea-Bissau. Missing data are denoted by '–'. KUD: kernel utilization distribution. CCL: curved carapace length

Year	Turtle ID	CCL (cm)	Tag type	Location type	Recording duration (d)	Locations within JVPMNP (%)	Locations within no-take zone (%)	Core area: 50% KUD (km^2)	Home range: 95% KUD (km^2)
2018	PTT60865	113.5	SPOT-375B	Argos	24.67	99.66	94.28	9.36	47.74
2018	PTT60868	91.0	SPOT-375B	Argos	21.42	99.61	87.98	7.65	52.13
2018	PTT60886	–	SPOT-375B	Argos	14.33	100.00	97.69	6.98	34.96
2018	PTT60887	105.0	SPOT-375B	Argos	82.33	97.98	75.33	10.90	74.11
2018	PTT60888	109.0	SPOT-375B	Argos	21.67	98.08	80.84	7.79	47.92
2018	PT60889	104.0	SPOT-375B	Argos	12.58	98.03	87.50	9.31	42.58
2018	PTT60890	98.5	SPOT-375B	Argos	4.08	100.00	100.00	6.47	32.31
2018	PTT60891	92.5	SPOT-375B	Argos	11.42	67.39	52.90	11.04	331.24
2018	PTT60892	106.0	SPOT-375B	Argos	10.92	93.18	69.70	10.61	59.71
2018	PTT60893	–	SPOT-375B	Argos	34.58	99.76	96.63	7.32	40.43
2018	PTT60894	87.0	SPOT-375B	Argos	43.50	90.63	69.60	17.84	170.49
2018	PTT60897	78.0	SPOT-375B	Argos	23.75	40.91	29.37	54.06	495.56
2018	PTT60898	95.0	SPOT-375B	Argos	9.67	98.29	91.45	8.25	61.89
2018	PTT60899	103.0	SPOT-375B	Argos	10.33	96.80	70.40	8.94	45.66
2018	PTT60900	102.0	SPOT-375B	Argos	48.75	96.93	83.11	17.16	138.70

Table S2.1. (continued)

Year	Turtle ID	CCL (cm)	Tag type	Location type	Recording duration (d)	Locations within JVPMNP (%)	Locations within no-take zone (%)	Core area: 50% KUD (km^2)	Home range: 95% KUD (km^2)
2019	0049-P	104.0	Arribada	GPS	5.33	100.00	100.00	5.30	22.85
2019	0056-P	90.0	Arribada	GPS	5.75	100.00	84.29	15.56	103.38
2019	0057-P	109.0	Arribada	GPS	9.08	100.00	100.00	4.50	19.48
2019	0058-P	100.0	Arribada	GPS	8.50	100.00	100.00	4.58	19.89
2019	0059-P	104.0	Arribada	GPS	5.00	100.00	95.08	6.53	28.38
2019	0060-P	101.0	Arribada	GPS	5.58	100.00	100.00	5.05	21.80
2019	0061-P	87.0	Arribada	GPS	5.50	100.00	100.00	4.77	20.55
2019	0064-P	99.0	Arribada	GPS	10.50	100.00	100.00	4.36	18.83
2019	0066-P	86.0	Arribada	GPS	5.92	100.00	100.00	4.91	21.15
2019	0067-P	102.0	Arribada	GPS	5.50	100.00	100.00	4.56	19.76
2019	PTT182450	104.3	FastGPS	Argos + GPS	59.00	100.00	94.64	6.39	35.30
2019	PTT182451	96.0	FastGPS	Argos + GPS	58.75	99.72	93.34	6.78	36.43
2019	PTT182452	98.5	FastGPS	Argos + GPS	56.00	98.37	87.07	9.10	86.02
2019	PTT182455	105.5	FastGPS	Argos + GPS	54.17	93.86	79.26	7.41	111.21
2019	PTT182456	102.0	FastGPS	Argos + GPS	72.00	98.96	95.03	6.78	35.61

Table S2.1. (continued)

Year	Turtle ID	CCL (cm)	Tag type	Location type	Recording duration (d)	Locations within JVPMNP (%)	Locations within no-take zone (%)	Core area: 50% KUD (km^2)	Home range: 95% KUD (km^2)
2019	PTT182457	99.5	FastGPS	Argos + GPS	47.67	95.64	75.04	17.07	130.50
2019	PTT182458	84.0	FastGPS	Argos + GPS	41.67	98.40	81.04	10.59	91.79
2019	PTT182459	106.5	FastGPS	Argos + GPS	24.67	95.96	73.40	14.17	133.20
2019	PTT182461	99.0	FastGPS	Argos + GPS	53.17	100.00	99.22	5.62	27.23
2020	PTT197137	105.0	FastGPS	Argos + GPS	15.42	100.00	100.00	5.72	27.67
2020	PTT197138	96.5	FastGPS	Argos + GPS	39.58	98.53	89.29	11.49	76.32
2020	PTT205277	111.2	FastGPS	Argos + GPS	32.08	97.41	78.50	11.97	103.16
2020	PTT205279	92.0	FastGPS	Argos + GPS	13.42	100.00	96.30	9.99	89.87
2020	PTT205281	97.0	FastGPS	Argos + GPS	39.83	96.03	81.21	7.03	31.25
2020	PTT205282	97.0	FastGPS	Argos + GPS	22.08	96.24	80.45	16.72	110.58
2020	PTT205284	103.5	FastGPS	Argos + GPS	71.50	92.90	71.25	16.09	167.37
2020	PTT205285	110.0	FastGPS	Argos + GPS	30.00	93.07	78.95	16.46	97.37
2020	PTT205287	85.0	FastGPS	Argos + GPS	24.25	99.32	84.25	17.63	114.59
2020	PTT205288	121.5	FastGPS	Argos + GPS	14.58	100.00	99.43	5.53	26.92
Mean ± SD		99.5 ± 8.8			27.50 ± 21.50	96.17 ± 10.00	86.45 ± 14.49	10.37 ± 7.96	79.63 ± 86.92

Table S2.2. Estimates for the general multiple linear models used to investigate the influence of the curved carapace length (CCL), nesting beach sector, date of tag deployment (day-of-year), recording duration and year on the extent of the 50 and 95% kernel utilization distribution (KUDs). **Bold** indicates significant values (*p* <0.05)

Response variables	Coefficients	Estimate	Std Error	t	*p*
50% KUD	CCL	0.82	0.57	-1.44	0.16
	Nesting beach sector FAR	1.41	2.20	0.64	0.53
	Nesting beach sector AO	-2.03	2.06	0.99	0.33
	Nesting beach sector CAB	0.90	2.11	-0.42	0.67
	Date of tag deployment	-2.27	1.19	-1.92	0.06
	Recording duration	1.05	0.63	1.66	0.11
	Year 2019	-6.98	2.57	-2.72	**<0.05**
	Year 2020	0.47	1.90	0.25	0.81
95% KUD	Nesting beach sector FAR	-4.82	22.06	0.22	0.83
	Nesting beach sector AO	-32.99	20.96	-1.57	0.12
	Nesting beach sector CAB	-22.72	20.40	-1.11	0.27
	Date of tag deployment	-12.10	10.02	-1.21	0.24
	Recording duration	15.91	6.30	2.53	**<0.05**
	Year 2019	-29.67	22.32	-1.33	0.19
	Year 2020	18.40	18.18	1.01	0.32

Table S2.3. ANOVA table from the multiple linear models predicting the effect of the tag type on the extent of the 50 and 95% kernel utilization distributions (KUDs). **Bold** indicates significant values (*p* <0.05)

Response variables	Explanatory variables	df	SS	MS	F	*p*
50% KUD	CCL	1	17.71	17.71	1.73	0.21
	Date of tag deployment	1	94.22	94.22	9.22	**<0.01**
	Recording duration	1	15.59	15.59	1.53	0.24
	Residuals	15	153.29	10.22	–	–
95% KUD	CCL	1	922.30	922.30	1.30	0.28
	Nesting beach sector	3	2931.80	977.30	1.37	0.30
	Date of tag deployment	1	14399.10	14399.10	20.25	**<0.001**
	Recording duration	1	3982.40	3982.40	5.60	**<0.05**
	Tag type	1	1477.10	1477.10	2.08	0.18
	Residuals	11	7820.40	710.90	–	–

Table S2.4. Estimates for the multiple linear models to test the tag type effect on the extent of the 50 and 95% kernel utilization distribution (KUDs). **Bold** indicates significant values (*p* <0.05)

Response variables	Coefficients	Estimate	Std Error	t	*p*
50% KUD	CCL	-1.01	0.77	-1.32	0.21
	Date of tag deployment	-5.88	1.83	-3.20	**<0.01**
	Recording duration	-4.31	1.82	-2.37	**<0.05**
95% KUD	CCL	-10.58	7.61	-1.39	0.19
	Nesting beach sector FAR	-30.29	30.38	-1.00	0.34
	Nesting beach sector AO	-29.42	37.60	0.78	0.45
	Nesting beach sector CAB	-55.20	31.02	-1.78	0.10
	Date of tag deployment	-44.95	29.41	-1.53	0.15
	Recording duration	-59.54	17.87	-3.33	**<0.01**
	FastGPS tags	78.39	56.84	1.38	0.20

Table S2.5. 50 and 95% kernel utilization distribution (KUDs) areas and overlap for two randomly selected inter-nesting intervals of 20 female green turtles tracked during the 2018, 2019 and 2020 breeding periods within the João Vieira-Poilão Marine National Park, Bijagós Archipelago, Guinea-Bissau. The overlap represents the proportion of the later randomly selected inter-nesting interval included in the first randomly selected inter-nesting interval

PTT	First randomly selected inter-nesting interval			Later randomly selected inter-nesting interval			KUDs intersect area and overlap			
	Identifier of the inter-nesting interval	50% KUD area (km^2)	95% KUD area (km^2)	Identifier of the inter-nesting interval	50% KUD area (km^2)	95% KUD area (km^2)	50% KUDs intersect area (km^2)	95% KUDs intersect area (km^2)	50% KUDs overlap (%)	95% KUDs overlap (%)
60865	1	9.15	45.32	2	8.75	48.40	7.21	41.30	82.41	85.32
60887	2	8.65	46.20	3	9.72	44.51	6.50	35.61	66.91	79.99
60893	1	7.41	41.86	2	6.68	32.12	6.06	31.04	90.67	96.63
60894	1	18.13	189.02	2	15.88	91.47	12.48	71.72	78.60	78.41
60900	3	15.35	70.48	4	14.23	151.73	12.54	61.84	88.11	40.75
182450	2	5.20	23.92	3	5.69	28.92	5.20	23.73	91.37	82.06
182451	3	6.51	31.61	4	6.45	30.29	6.00	27.96	93.01	92.31
182452	1	11.14	93.44	2	7.92	41.01	7.61	41.01	96.08	100.00
182455	2	8.67	60.84	3	8.19	58.31	7.08	49.48	86.49	84.86
182456	3	5.35	23.11	6	6.24	27.70	4.87	22.72	78.02	82.02
182457	3	17.52	98.77	4	15.62	109.38	9.95	63.63	63.68	58.17

Table S2.5. (continued)

PTT	First randomly selected inter-nesting interval			Later randomly selected inter-nesting interval			KUDs intersect area and overlap			
	Identifier of the inter-nesting interval	50% KUD area (km^2)	95% KUD area (km^2)	Identifier of the inter-nesting interval	50% KUD area (km^2)	95% KUD area (km^2)	50% KUDs intersect area (km^2)	95% KUDs intersect area (km^2)	50% KUDs overlap (%)	95% KUDs overlap (%)
182458	1	15.14	99.45	3	8.54	69.54	8.54	64.39	100.00	92.60
182459	1	11.25	75.64	2	17.22	138.86	10.64	56.41	61.81	40.63
182461	3	5.12	22.32	4	4.98	21.80	4.48	21.02	89.87	96.44
197138	2	9.46	60.07	3	12.24	89.99	9.46	56.66	77.27	62.97
205277	1	9.65	98.70	2	9.45	87.43	8.84	73.33	93.50	83.87
205281	1	19.19	112.72	3	12.71	82.25	10.78	66.77	84.77	81.18
205284	4	11.78	95.15	6	6.88	41.28	6.88	40.80	100.00	98.83
205285	1	19.65	109.31	2	13.76	79.23	10.64	72.40	77.34	91.38
205287	1	11.34	80.47	2	21.86	125.67	8.38	69.32	38.33	55.16
Mean ± SD		11.28 ± 4.72	73.92 ± 40.58		10.65 ± 4.58	69.99 ± 39.20	8.21 ± 2.42	49.56 ± 18.29	81.91 ± 15.11	79.18 ± 18.18

Table S2.6. Number and percentage of locations occurring within the João Vieira-Poilão Marine National Park (JVPMNP), according to the type of bio-logging devices deployed on 44 female green turtles during the 2018, 2019 and 2020 breeding periods

Year	Tag type	Number of turtles	Number of locations	Number of locations within the JVPMNP	Locations within the JVPMNP (%)	Number of locations within the no-take zone	Locations within the no-take zone (%)
2018	SPOT-375B	15	4503	4176	92.74	3512	84.10
2019	Arribada	10	810	810	100	796	98.27
2019 + 2020	FastGPS	19	9257	9016	97.34	7933	85.70
2019	FastGPS	9	5614	5507	98.09	4942	88.03
2020	FastGPS	10	3643	3509	96.32	2991	82.10

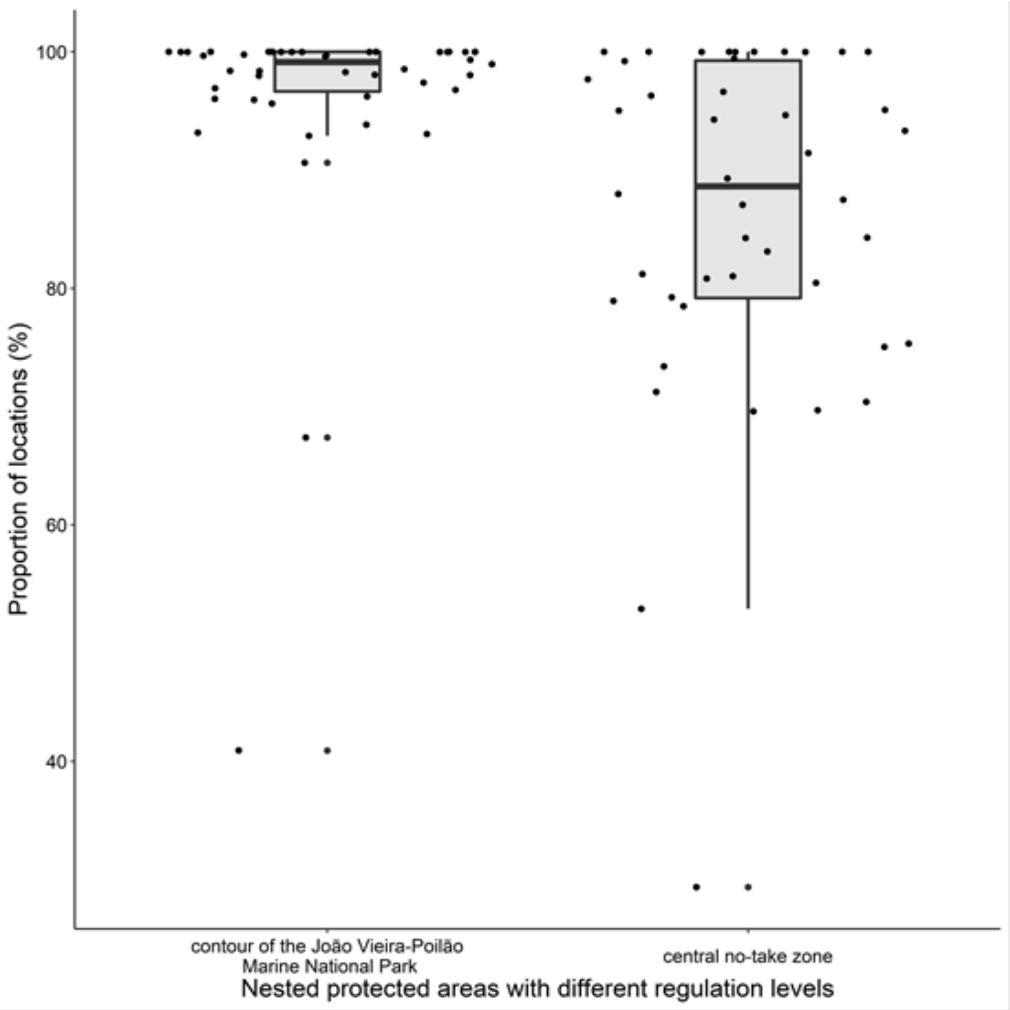

Fig. S2.1. Percentage of locations of 44 female green turtles tracked within the João Vieira-Poilão Marine National Park, during the breeding period. The João Vieira-Poilão Marine National Park includes a central no-take zone (right). Each dot corresponds to one individual

APPENDIX: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 3

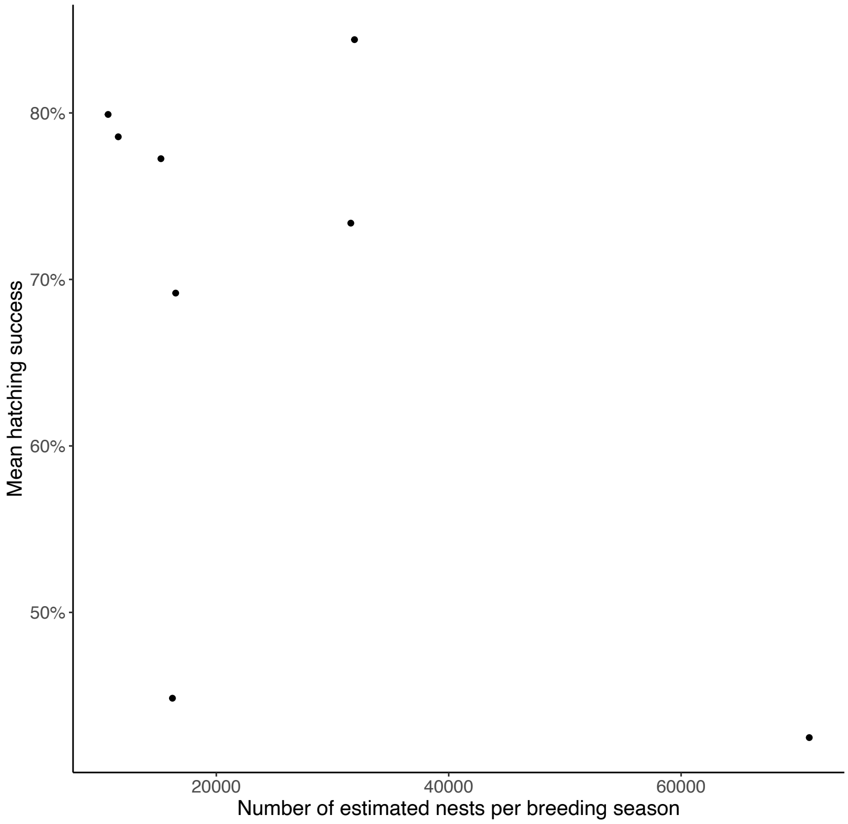

Fig. S3.1. Relation between the mean hatching success (excluding all lost clutches from the calculation) and the number of estimated green turtle nests per breeding season from 2015 through 2022 on Poilão, Bijagós Archipelago, Guinea-Bissau

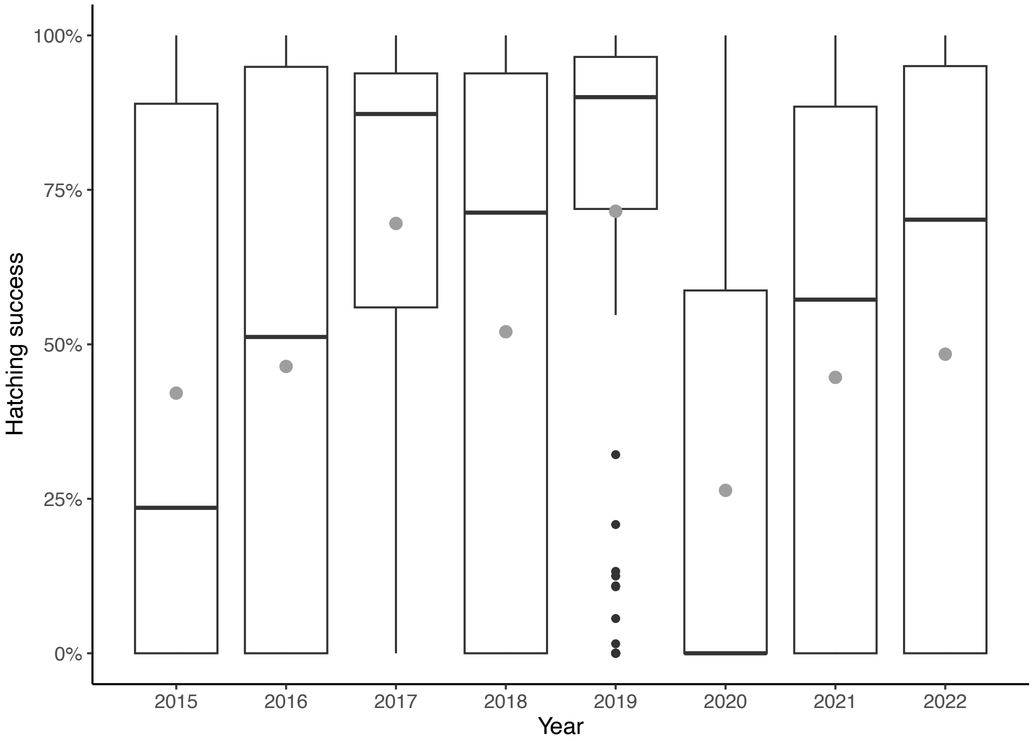

Fig. S3.2. Green turtle hatching success between 2015 and 2022 on Poilão, Bijagós Archipelago, Guinea-Bissau, encompassing all monitored nests, including those that were lost and assigned a hatching success rate of zero. Boxplots include the median, 25th and 75th percentiles and outliers. The grey dots depict the mean hatching success for each year

APPENDIX: SUPPLEMENTARY MATERIALS AND METHODS

CHAPTER 4

Table S4.1. Mean (± SD) isotopic signatures for samples of plants, crabs and fishes. Plant species include coinvines (*Dalbergia ecastaphyllum*) and baobabs (*Adansonia digitata*), crab species include tufted ghost crabs (*Ocypode cursor*) and African rainbow crabs (*Cardisoma armatum*), and fish species include sea catfishes (*Carlarius* spp.) and crevalle jacks (*Caranx hippos*). Nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopic ratios are shown for fishes classified as 'wide gape'. 'NA' denotes not applicable

Species	Year	Location	Tissue	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)
Coinvines	2021	João Vieira	Leaves	-1.5 ± 1.5	-30.6 ± 0.6
		Poilão	Leaves	3.3 ± 4.3	-30.4 ± 2.0
	2022	João Vieira	Leaves	0.3 ± 3.0	-29.2 ± 1.3
		Poilão	Leaves	4.6 ± 3.4	-31.2 ± 0.8
	2023	João Vieira	Leaves	-0.1 ± 0.9	-30.2 ± 0.5
		Poilão	Leaves	6.5 ± 1.9	-30.6 ± 0.7
Baobabs	2021	João Vieira	Leaves	4.1 ± 2.2	-31.2 ± 1.3
		Poilão	Leaves	5.1 ± 3.0	-31.6 ± 0.6
	2022	João Vieira	Leaves	4.0 ± 1.2	-29.6 ± 0.7
		Poilão	Leaves	6.6 ± 2.4	-31.9 ± 0.8
	2023	João Vieira	Leaves	8.4 ± 0.9	-31.6 ± 0.6
		Poilão	Leaves	6.4 ± 2.2	-31.8 ± 1.0
Tufted ghost crabs	2021	João Vieira	Muscle	NA	NA
		Poilão	Muscle	15.2 ± 0.7	-13.3 ± 0.8
	2022	João Vieira	Muscle	12.2 ± 1.1	-18.7 ± 1.4
		Poilão	Muscle	15.2 ± 0.6	-13.5 ± 0.6
African rainbow crabs	2021	João Vieira	Muscle	8.5 ± 0.9	-24.8 ± 0.9
		Poilão	Muscle	7.9 ± 1.7	-24.4 ± 0.3
	2022	João Vieira	Muscle	NA	NA
		Poilão	Muscle	NA	NA

Table S4.1. (continued)

Species	Year	Location	Tissue	δ15N (‰)	δ13C (‰)
Sea catfishes	2021	João Vieira	Muscle	18.2 ± 0.5	-13.7 ± 0.7
			Blood	16.1 ± 0.5	-14.2 ± 0.6
		Poilão	Muscle	18.4 ± 1.0	-13.9 ± 0.8
			Blood	16.0 ± 0.4	-14.6 ± 0.9
	2022	João Vieira	Muscle	16.3 ± 0.4	-14.9 ± 0.8
			Blood	16.4 ± 1.5	-15.0 ± 1.8
		Poilão	Muscle	16.3 ± 0.4	-14.5 ± 0.6
			Blood	15.4 ± 0.5	-14.2 ± 0.7
Crevalle jacks	2021	João Vieira	Muscle	17.1 ± 0.3	-13.2 ± 0.7
			Blood	16.2 ± 0.4	-13.4 ± 1.0
		Poilão	Muscle	17.1 ± 0.9	-14.7 ± 0.8
			Blood	17.0 ± 0.8	-14.6 ± 1.0
	2022	João Vieira	Muscle	17.4 ± 0.7	-13.1 ± 2.5
			Blood	17.8 ± 1.7	-14.1 ± 1.1
		Poilão	Muscle	17.5 ± 0.6	-14.8 ± 0.2
			Blood	17.5 ± 1.2	-14.9 ± 0.6

Table S4.2. Simple linear regressions between foliar nitrogen isotopic ratio ($\delta^{15}N$) and the nitrogen content (%N) for coinvines *Dalbergia ecastaphyllum* and baobabs *Adansonia digitata* by year on João Vieira and Poilão Islands. **Bold** indicates significant values (p <0.01 or p <0.05)

Species	Year	Location	Simple linear regression
Coinvines	2021	João Vieira	adjusted $r^2 = 0.49$, $n = 5$, $F_{1,3} = 4.77$, $p = 0.12$
		Poilão	**adjusted $r^2 = 0.78$, $n = 5$, $F_{1,3} = 14.98$, $p = 0.031$**
	2022	João Vieira	adjusted $r^2 = -0.31$, $n = 5$, $F_{1,3} = 0.06$, $p = 0.82$
		Poilão	adjusted $r^2 = 0.15$, $n = 5$, $F_{1,3} = 1.72$, $p = 0.28$
	2023	João Vieira	adjusted $r^2 = -0.03$, $n = 8$, $F_{1,6} = 0.83$, $p = 0.40$
		Poilão	adjusted $r^2 = 0.26$, $n = 8$, $F_{1,6} = 3.49$, $p = 0.11$
Baobabs	2021	João Vieira	**adjusted $r^2 = 0.80$, $n = 5$, $F_{1,3} = 17.42$, $p = 0.025$**
		Poilão	**adjusted $r^2 = 0.90$, $n = 5$, $F_{1,3} = 35.17$, $p = 0.010$**
	2022	João Vieira	adjusted $r^2 = -0.33$, $n = 5$, $F_{1,3} = 0.00$, $p = 0.98$
		Poilão	adjusted $r^2 = 0.64$, $n = 5$, $F_{1,3} = 8.02$, $p = 0.07$
	2023	João Vieira	adjusted $r^2 = -0.02$, $n = 8$, $F_{1,6} = 0.85$, $p = 0.39$
		Poilão	adjusted $r^2 = -0.00$, $n = 8$, $F_{1,6} = 1.00$, $p = 0.36$

Table S4.3. Spearman's rank correlation coefficient between muscle nitrogen isotopic ratio ($\delta^{15}N$) and carapace width (CW) for tufted ghost crabs *Ocypode cursor* and African rainbow crabs *Cardisoma armatum* by year on João Vieira and Poilão Islands. Data represents combined information from both islands. **Bold** indicates significant values (p <0.05)

Species	Year	Spearman's rank correlation coefficient
Tufted ghost crabs	2021	rs = 0.52, $n = 6$, $p = 0.29$
	2022	**rs = 0.46, $n = 24$, $p = 0.025$**
African rainbow crabs	2021	rs = 0.35, $n = 12$, $p = 0.26$

Table S4.4. Spearman’s rank correlation coefficient between muscle and blood nitrogen isotopic ratios ($\delta^{15}N$) and fish fork length (FL, cm) for sea catfish *Carlarius* spp*.* and crevalle jacks *Caranx hippos* by year on João Vieira and Poilão Islands. Data represents combined information from both islands. **Bold** indicates significant values (*p* <0.01 or *p* <0.05)

Species	Year	Tissue	Spearman’s rank correlation coefficient
Sea catfishes	2021	Muscle	rs = 0.23, *n* = 47, *p* = 0.12
		Blood	**rs = 0.73, *n* = 12, *p* = 0.007**
	2022	Muscle	rs = 0.19, *n* = 28, *p* = 0.35
		Blood	rs = 0.03, *n* = 25, *p* = 0.89
Crevalle jacks	2021	Muscle	rs = 0.17, *n* = 25, *p* = 0.41
		Blood	**rs = -0.52, *n* = 17, *p* = 0.031**
	2022	Muscle	rs = 0.21, *n* = 22, *p* = 0.35
		Blood	rs = -0.08, *n* = 22, *p* = 0.72

Table S4.5. Spearman’s rank correlation coefficient between the numerical frequency of each prey items groups and fish fork length (FL, cm) for both ‘restricted gape’ and ‘wide gape’ sea catfishes *Carlarius* spp. by year on João Vieira and Poilão islands. Data represents combined information from both islands. Groups of prey items: ‘green turtle items’ (green turtle *Chelonia mydas* eggs and hatchlings), ‘benthic fauna’ (crabs not identified, marbled swimcrabs *Callinectes marginatus*, shrimps not identified, ophiuroids not identified, sea cucumbers not identified and ball sea cucumbers *Phyllophorus* sp.), and ‘nektonic fauna’ (fish not identified, Madeiran sardinella *Sardinella maderensis* and Lesser African threadfin *Galeoides decadactylus*). **Bold** indicates significant values (p <0.001)

Species	Mouth gape	Year	Group of prey items	Spearman’s rank correlation coefficient
Sea catfishes	Restricted	2021	Green turtle items	–
			Benthic fauna	rs = -0.20, *n* = 9, *p* = 0.61
			Nektonic fauna	rs = 0.00, *n* = 9, *p* = 1.00
		2022	Green turtle items	–
			Benthic fauna	–
			Nektonic fauna	–
	Wide	2021	**Green turtle items**	**rs = 0.60, *n* = 38, p <0.001**
			Benthic fauna	rs = 0.27, *n* = 38, *p* = 0.11
			Nektonic fauna	rs = 0.05, *n* = 38, *p* = 0.75
		2022	Green turtle items	rs = 0.32, *n* = 27, *p* = 0.11
			Benthic fauna	rs = -0.09, *n* = 27, *p* = 0.64
			Nektonic fauna	rs = -0.05, *n* = 27, *p* = 0.81