THE SPATIAL ECOLOGY OF MEDITERRANEAN MARINE TURTLES: INSIGHTS FROM STABLE ISOTOPE ANALYSIS, SATELLITE TELEMETRY, AND ENVIRONMENTAL OBSERVATIONS

Submitted by

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I certify that all material in this thesis that is not my own work has been identified and that no material has been previously submitted and approved for the award of degree by this or any other University.

Signed:

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Loggerhead turtle satellite tracked from Alagadi Beach, North Cyprus, during the 2017 field season

Photo credit: Olkan Erguler

ABSTRACT

Understanding the spatial and foraging ecology of marine migrants is challenging, due to the vast distances travelled and the numerous habitats occupied within a dynamic seascape. Mediterranean marine turtles migrate thousands of kilometers and face numerous threats, including bycatch, in their marine realm. To help inform targeted conservation, this complex marine ecology must be better understood. This thesis focuses on Mediterranean loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*). By complementing stable isotope analysis (SIA), satellite telemetry, and environmental observations, this thesis aims to enhance our understanding of the complexities of marine turtle spatial and foraging ecology, as well as determine how future climate conditions may influence their habitat use.

In **Chapter 1**, I introduce the importance of conserving marine migrants and discuss the current knowledge of marine turtle spatial and foraging ecology as well as threats faced, with particular emphasis on Mediterranean loggerhead and green turtles. By conducting an extensive review in **Chapter 2**, I demonstrate how SIA has been used to enhance our understanding of marine turtle ecology, as well as help inform conservation initiatives. I also highlight knowledge gaps (for example, bias in the species studied) and provide recommendations for future SIA studies (for example, following standardised protocols), and use this information to inform latter chapters. In **Chapter 3**, using SIA I highlight the ecological complexity of juvenile Mediterranean loggerhead turtles, demonstrating there are inter- and intra-population variations in ecology, and that region- and habitat-specific fisheries management is required. In **Chapter 4**, I identify the foraging grounds for two major Mediterranean loggerhead turtle populations, demonstrate foraging site fidelity over decades, show the proportion of females recruiting from each foraging region does not differ across the multi-decadal study, and suggest site-specific management would be beneficial. Finally, in **Chapter 5**, I show that migratory dive behaviours of loggerhead and green turtles are influenced by changes in environmental conditions (e.g. wave height and temperature) and that the species-specific migratory corridors used may be due to factors such as feeding preference and physiology, rather than species-specific environmental tolerances, suggesting dynamic and species-specific conservation is required. In **Chapter 6**, I summarise and discuss the findings from this thesis within the wider context. In conclusion, this thesis emphasises the complexities of marine turtle spatial ecology, shows that habitat use will likely differ under future climate scenarios, and suggests targeted and dynamic conservation is required for effective long term conservation.

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AUTHOR'S DECLARATION

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JH drafted the chapter and AB and JS guided the writing.

Chapter 2: Global review and inventory: how stable isotopes are helping us understand ecology and inform conservation of marine turtles

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AB, BG, JS, SW, and WF conceived the project ideas; JH collected and analysed the data and drafted the manuscript; AB, BG, and JS guided the writing with contributions from all authors. All authors read and approved the final manuscript. Three anonymous reviewers improved the manuscript during peer review prior to publication.

Chapter 3: Foraging ecology of Mediterranean juvenile loggerhead turtles: insights from C and N stable isotope ratios

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Chapter 4: Spatial ecology of loggerhead turtles: insights from stable isotope markers and satellite telemetry

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CHAPTER 1: GENERAL INTRODUCTION

Marine migrants roam vast areas of the oceans, often occupying different habitats on a seasonal basis. Consequently, identifying and understanding their movement patterns, critical areas of habitat use, and potential risks to their survival can be challenging. Their reliance upon different ecosystems during different stages of their lives increases their vulnerability to climate change and direct anthropogenic pressures (Robinson et al., 2009). Therefore, to protect them, it is crucial to understand their spatial and temporal distribution, behaviour, and how they interact and are influenced by their environment. This collective information will facilitate effective and dynamic management of all marine migrants.

Satellite telemetry and stable isotope analysis (SIA) are powerful tools used to investigate the spatial ecology of marine migrants. Satellite telemetry provides fine-scale movement data at an individual level (Godley et al., 2008), and when complemented with SIA, these tracking tools can provide information at a population level enabling better informed conservation plans. Natural isotope gradients occur throughout the oceans due to variations in nutrient cycling (DeNiro & Epstein 1978). For example, within the Mediterranean Sea the Adriatic Sea has low $\delta^{13}C$ values and high $\delta^{15}N$ values compared to other regions, due to the influence of terrestrial organic matter and highly enriched ^{15}N agricultural run-off from major river systems (Degobbis & Gilmartin, 1990). The geographical location food was ingested by an individual relates to the isotopes within the environment and are reflected in low-metabolically active tissues of the individual (DeNiro & Epstein 1978). The ratios of isotopes within tissue samples can be measured using SIA and in turn used as geographic markers at a population level. SIA and satellite telemetry methods have been widely used to answer spatial conservation questions regarding key marine indicator species, including marine mammals (e.g. Newsome et al. 2010), elasmobranchs (e.g. Shiffman et al. 2012, Bird et al. 2018), seabirds (e.g. Forero & Hobson 2003, Roscales et al. 2011), and marine turtles (Haywood et al., 2019).

Marine turtles in particular are an important study system for investigating the spatial ecology of marine migrants. They are considered as ‘flagship’ species as well as key indicator species of ecosystem function and health (Aguirre & Lutz, 2004), have complex life histories spanning multiple habitats (Miller 1997, Fig 1), differing diets dependent on life stage (e.g. Snover, 2008), and migrations of thousands of kilometers across dynamic seascapes (e.g. Luschi et al., 2003; James et al., 2005; Godley et al., 2008). Of the seven extant marine turtle species, green turtles (*Chelonia mydas*) and loggerhead turtles (*Caretta caretta)* are found circumglobally in nearly all the oceans of the world. However, due to many anthropogenic pressures, these marine turtles are listed on the International Union for Conservation of Nature (IUCN) Red List as Endangered on a global scale.

The level of natural and anthropogenic threats faced is dependent on life stage and location, and therefore, a diverse approach to conservation is required (Wallace et al., 2011). Understanding the complexities of marine turtle spatial and foraging ecology, as well as how future climate conditions will influence their habitat use, are therefore considered research priorities (Hamann et al., 2010; Rees et al., 2016).

MARINE TURTLE LIFE CYCLE

Marine turtles have complex life history strategies, with species-specific differences occurring due to their adaptation to different ocean habitats during their evolutionary history (Plotkin, 2003). In general, the typical green and loggerhead turtle life cycle follows the oceanic-neritic developmental pattern (Bolten, 2003), with ontogenetic shifts in habitat and diet (Fig 1). Beginning at the nest, hatchlings emerge and enter their 'frenzied phase', entering the sea and swimming directly out to the ocean (Wyneken & Salmon, 1992). Hatchlings actively swim to reach offshore ocean currents in oceanic waters (water depths > 200 m) where they likely have higher food availability and reduced predation. Post-hatchlings remain in the near-surface waters, passively drifting with surface ocean currents as they grow in size, becoming juveniles over a period known as their 'lost years' (Carr, 1986). During this oceanic phase, juveniles remain epi-pelagic, foraging on gelatinous prey, such as, jellyfish and tunicates (Bjorndal, 1997). The duration of this oceanic phase differs between species and populations (e.g. Avens et al., 2013; Turner Tomaszewicz et al., 2017), potentially driven by differences in food and habitat availability (Bolten, 2003).

After the oceanic phase, juveniles undergo an ontogenetic shift, moving to neritic habitats where they complete their development and their foraging strategies become specialized. The duration of this transitional phase again differs among and within populations, either occurring relatively rapidly or gradually over several years (e.g. Ramirez et al., 2015; Vélez-Rubio et al., 2016; Di Beneditto et al., 2017) and at a range of sizes, for example at 0.25 m in length for loggerhead turtles in the Adriatic Sea (Lazar et al., 2008) and 0.67 m in the Amvrakikos Gulf (Rees et al., 2013). During this phase an associated dietary shift is likely, with turtles greater in size having greater diving capabilities, enabling benthic prey to be accessed. Loggerhead turtles are opportunists, foraging on invertebrates (for example, crustaceans and molluscs), as well as fish and sponges in their neritic habitats, and green turtles are generally herbivores, foraging on seagrass and macroalgae (Bjorndal, 1997), but are in some cases omnivorous (e.g. Piovano et al., 2020).

Sexual maturity is reached in neritic foraging grounds (e.g. Rees et al., 2013), and when mature, males and females make cyclic-seasonal migrations often of considerable distances to mating/nesting grounds (Casale et al., 2018). Females will lay several clutches over the nesting season with an inter-nesting interval of around two to three weeks (Broderick et al., 2003, Stokes et al., 2014), after which the adults will return to their foraging grounds, to which they show high fidelity (Broderick et al., 2007; Bradshaw et al., 2017; Shimada et al., 2020). Adults then remain in their foraging grounds for several years (1-6 years for loggerhead and 2-6 years for green turtles), building lipid reserves, before repeating their reproductive migrations (Broderick et al., 2001).

Within species exceptions have been documented, for example some Pacific populations of loggerhead and green turtles have been reported to remain in oceanic foraging grounds throughout their lives (e.g. Hatase et al., 2002, 2006), whilst some populations in the Pacific and Mediterranean are thought to move between oceanic and neritic habitats interchangeably (e.g. Casale et al., 2008; Piovano et al., 2020).

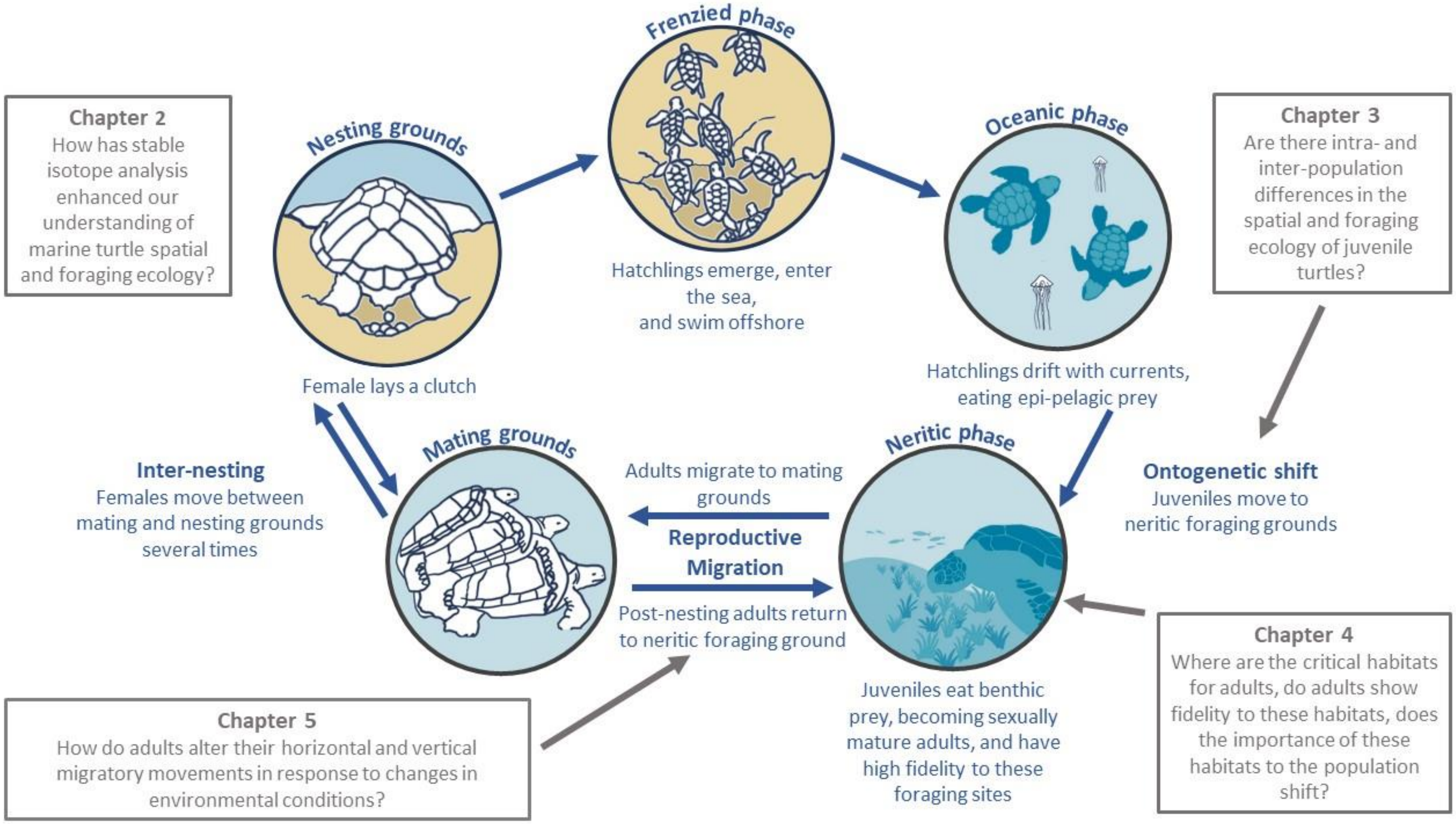

Figure 1. The typical marine turtle life cycle with research questions investigated within this thesis indicated.

MEDITERRANEAN TURTLES

The Mediterranean supports nesting populations of loggerhead and green turtles, whilst leatherback, olive ridley, and Kemp's ridley turtles, only enter the basin to forage. Abundance estimates for these Mediterranean nesting populations are between 1.2 and 2.4 million loggerhead turtles, with 16,000 adults, and between 0.3 and 1.3 million green turtles, with 3000 adults (Casale & Heppell, 2016). Compared to global populations, Mediterranean loggerhead turtles are considerably smaller in body size (for example, straight carapace length = 0.79 m in Greece, 0.91 m in Florida, and 0.93 m in Brazil, Tiwari & Bjorndal, 2000), whilst green turtles are at the lower size range (Seminoff et al., 2015). Loggerhead turtle nesting grounds are distributed around the east Mediterranean basin, with major rookeries in Greece, Turkey, Libya, and Cyprus (Fig 2; Casale et al., 2018). In comparison, there are far fewer green turtle nesting grounds with major sites in Turkey, Cyprus, and Syria (Fig 2; Casale et al., 2018).

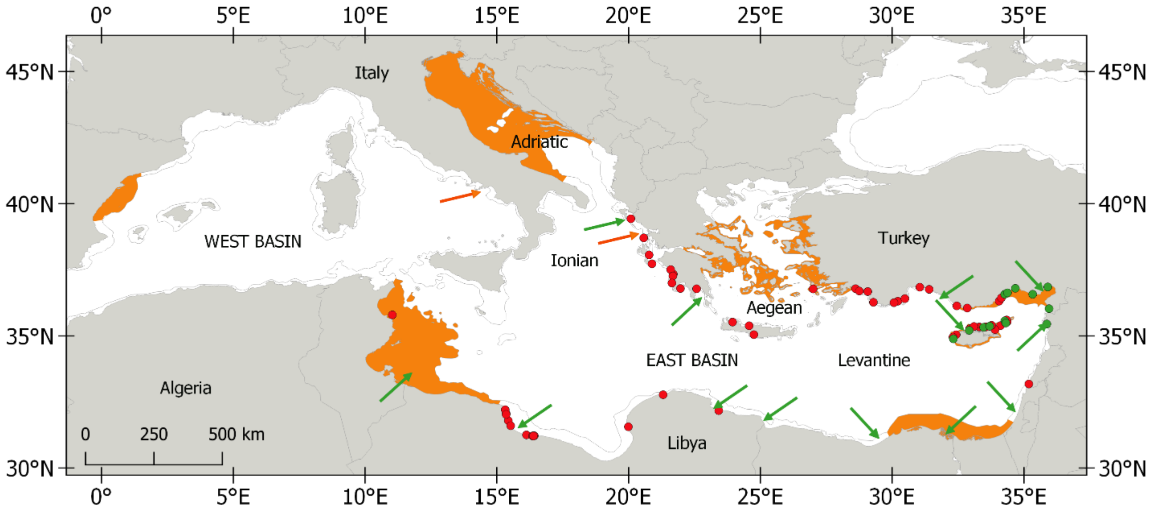

Figure 2. Nesting and foraging grounds of Mediterranean loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*). Points represent nesting grounds (red = loggerheads, green = green turtles). Shaded areas and arrows represent foraging grounds (orange = loggerheads, green = green turtles). 200 m isobath is indicated (grey line). Adapted from Casale et al. (2018).

Due to the inaccessibility of their marine habitat, understanding their distribution and habitat use in the marine realm is challenging. The location of the post-hatchling oceanic phase is unknown in the Mediterranean, however, hatchling dispersal simulation models suggest for loggerhead turtles, the east

Mediterranean basin and the Adriatic Sea are potential oceanic nursery habitats, with dispersal to western Mediterranean unlikely. The Levantine basin is an important nursery ground for green turtles (Casale & Mariani, 2014; reviewed in Casale et al., 2018). Juvenile loggerhead turtles are thought to be distributed across the Mediterranean during their oceanic phase, although most commonly within the eastern basin (Clusa et al., 2014), and juvenile green turtles are also thought to reside within the eastern basin, with the majority in the Levantine Sea (Casale et al., 2018).

Neritic foraging grounds are located around the east Mediterranean basin, as well as the Adriatic Sea, Aegean Sea, and the Spanish continental shelf for loggerhead turtles, whilst green turtle foraging grounds are thought to be limited to the east Mediterranean basin (Fig 2; Casale et al., 2018). Within the Mediterranean, recruitment of juvenile loggerhead turtles to neritic foraging grounds differs with region. In some regions, the ontogenetic shift to neritic grounds occurs at just 0.25 m in body size (e.g. Casale et al., 2008). For these individuals, the ontogenetic shift is thought to be very gradual, using both oceanic and neritic grounds interchangeably (Casale et al., 2008). In other areas, recruitment to neritic grounds occurs once loggerhead turtles are larger (over 0.65 m), with the shift occurring more abruptly (e.g. Rees et al., 2013; Snape et al., 2013). Loggerhead turtles have also been reported to remain oceanic foragers, never recruiting to neritic habitats (e.g. Schofield et al., 2010; Haywood et al., 2020). Green turtles recruit to neritic grounds at around 0.30 m in size, which is similar to other global populations (Cardona et al., 2010).

The body size of adult marine turtles differs with nesting population. The loggerhead turtle rookery-weighted mean size at sexual maturity is around 0.80 m for the Mediterranean (Casale et al., 2005; Casale & Heppell, 2016), but those nesting in North Cyprus are considerably smaller, reaching sexual maturity and nesting at only 0.64 m (mean = 0.72 m, Omeyer et al., 2018). Size at sexual maturity for green turtles is larger than loggerhead turtles starting at around 0.73 m (mean = 0.86 m, Omeyer et al., 2018). Age of sexual maturity is estimated at 25 years of age for loggerhead turtles in the Mediterranean (Casale & Heppell, 2016), whilst age-of-maturity remains unknown for green turtles (Casale et al., 2018). Reproductive longevity of green and loggerhead turtles has been recorded up to 25 years in the Mediterranean (Omeyer et al., 2019).

ANTHROPOGENIC THREATS

Marine migrants are considered some of the most threatened species globally, and their removal could have significant ecosystem wide impacts (Lascelles et al., 2014). Threats are relatively similar across marine migrant taxa and include; habitat degradation, direct exploitation, pollution, fisheries bycatch, and climate change (Lascelles et al., 2014), which are resulting in drastic declines in marine mammals (Schipper et al., 2008), sea birds (Croxall et al., 2012), marine turtles (Casale et al., 2018), and sharks (Dulvy et al., 2014). To successful manage marine migrants, understanding the cumulative effects of multiple pressure across their extensive range is crucial (Lascelles et al., 2014).

Marine migrants are particularly vulnerable to climate change, as shifts in ocean climate are likely causing environmentally driven changes in their spatial ecology and behaviour (Robinson et al., 2009). In addition, climate driven locational shifts in human activities could increase overlap with migrating species (e.g. Southall et al., 2006). Despite this, research and conservation strategies are often static, rarely taking environmental variability into consideration. It is therefore important to determine how marine migrants alter their spatial ecology and behaviour to changes in environmental conditions to identify what may happen under future climate scenarios (Bates et al., 2018).

Marine turtles are the most threatened marine migrant group (Lascelles et al., 2014). Climate change is the main indirect threat and bycatch the main direct anthropogenic threat (Wallace et al., 2011), with global marine turtle bycatch rates estimated to be higher than marine mammals and seabirds (Lewison et al., 2014). Other threats to marine turtles include direct take, coastal development, pollution, and pathogens, although these are considered region dependent (Donlan et al., 2010; Lascelles et al., 2014).

Mediterranean marine turtles face similar threats to those globally (Casale et al., 2018), however, the Mediterranean Sea has very high concentrations of contaminants (Casale et al., 2018), and plastic ingestion was found to be higher in Mediterranean populations in comparison to others (Duncan et al., 2019). As marine turtles are key indicator species (Aguirre & Lutz, 2004), this suggests the ecosystem function and health of the Mediterranean is likely detrimentally impacted. Similarly, bycatch rates are amongst the highest globally (Casale, 2011). It is estimated approximately 132,000 marine turtles are caught in fisheries in the Mediterranean each year resulting in 44,000 deaths annually (Casale, 2011). Pelagic longline, bottom trawl, set net, and demersal longline are the main gear types causing bycatch (Casale, 2011). Fishing gear and intensity are region and habitat specific, so the susceptibility of marine turtles differs according to population variations in spatial and foraging ecology (Casale, 2011). This complicates conservation management and requires region-specific management approaches within the Mediterranean. The Mediterranean is a semi-enclosed sea and therefore is particularly susceptible to changes in sea temperature. In addition, increased extreme weather events will occur globally (IPCC, 2019). With species within the Mediterranean unable to shift latitudinally due to the seas enclosed nature, there is a need to protect existing habitats and dynamically shift management strategies with changes in ocean climates.

Mediterranean loggerhead and green turtle populations are designated as Regional Management Units, with loggerhead turtles assigned as low risk but under high threat and green turtles as both high risk and high threat (Wallace et al., 2011). Under the IUCN Red List, there is no regional assessment for the Mediterranean green turtle subpopulation, whilst Mediterranean loggerhead turtles are listed as Least Concern, however, this listing is likely the direct result of extensive and intensive conservation, which if stopped, would likely cause a rapid population decline and uplisting of conservation threat level (Casale, 2015). Therefore, it has been suggested that the status of both species be considered as ‘conservation dependent” (Casale, 2015). Despite major threats within their marine realm, conservation and conservation-driven research has historically been targeted to the easily accessible nesting grounds (Hamann et al., 2010). However, this is only protecting a small proportion of their life cycle (~8.3% of an adult females’ time is spent at the nesting ground, Hays et al., 2014). Research to help inform conservation in their critical marine habitats throughout their life cycle would help protect the population as a whole.

Despite intensive conservation efforts on the nesting beaches, nest counts in Mediterranean rookeries are not increasing as rapidly as expected. Therefore, alternative conservation approaches, such as conserving critical marine habitats for all life stages, are considered essential (Casale et al., 2018). However, the majority of the sea turtle life cycle occurs in cryptic marine habitats which has resulted in large knowledge gaps in their marine spatial ecology. Increasing our understanding of the distribution, migratory connectivity, and how environmental conditions influence the spatial and temporal ecology of marine turtles are therefore considered research priorities for Mediterranean marine turtles (Hamann et al., 2010; Rees e al., 2016).

THESIS OVERVIEW

This thesis **'The spatial ecology of Mediterranean marine turtles: insights from stable isotope analysis, satellite telemetry, and environmental observations'** investigates the ecology of juvenile and adult Mediterranean loggerhead and green turtles. Through four chapters, written as independent units of study, I identify critical marine habitats for these elusive marine migrants, demonstrate intra- and inter-population differences in spatial and foraging ecology, and show that habitat use and behaviour will likely differ under future climate scenarios.

To investigate the spatial ecology of marine migrants I use multiple research methodologies, including; stable isotope analysis (SIA), a forensic method used to investigate the spatial, foraging, and reproductive ecology of marine migrants to inform conservation approaches. How this powerful tool has been used to enhance our understanding of marine turtles is extensively reviewed in **Chapter 2: 'Global review and inventory: how stable isotopes are helping us understand ecology and inform conservation of marine turtles'.** By summarising all current knowledge, I show how SIA has helped highlight the considerable flexibility and ecological complexity in the life histories of marine turtles and informed conservation initiatives by identifying threats faced. I highlight knowledge gaps and provide recommendations for future SIA studies.

In **Chapter 3: 'Foraging ecology of Mediterranean juvenile loggerhead turtles: insights from C and N stable isotope ratios',** I highlight the ecological complexity of juvenile Mediterranean loggerhead turtles. I use SIA to determine if there are inter- and intra-population variations in foraging and spatial ecology of juvenile loggerhead turtles to help inform region-specific fisheries management. Sex-specific differences were not observed suggesting females and males exploit similar foraging strategies and in turn are susceptible to similar threats. I show juvenile ecology differs between foraging regions, with some populations likely shifting to neritic habitats as they grow, while others continue to use neritic and oceanic habitats interchangeably. The susceptibility of these populations to fisheries bycatch will therefore likely differ, hence, region-specific and habitat-specific fisheries management will be required.

In **Chapter 4: 'Spatial ecology of loggerhead turtles: insights from stable isotope markers and satellite telemetry'**, I use satellite telemetry to provide detailed movement data for marine migrants in inaccessible habitats, enabling critical habitats to be identified. I complement satellite telemetry with SIA, to infer habitat use at a population level, identifying the foraging grounds for two major Mediterranean nesting populations. This work identifies a relatively small geographical region that supported a large proportion of females. I demonstrate foraging site fidelity over decades and show the proportion of nesting females recruiting from each foraging region does not differ across the multi-decadal study. In turn, this research suggests site-specific conservation to this specific region would increase both the survival of individuals in this foraging ground for the majority of their life cycle as well as protect a large proportion of two major Mediterranean loggerhead turtle rookeries.

In **Chapter 5: 'Marine turtles alter their migratory behaviour in response to environmental conditions',** I evaluate satellite remotely sensed and model re-analysis data in relation to the vertical and horizontal migratory behaviours of nesting loggerhead and green turtles to determine how they respond to local changes in environmental conditions. I show that migratory dive behaviours are influenced by changes in oceanographic conditions, that migratory routes are likely a balance between minimising energy expenditure and remaining in favourable conditions, and that the species-specific migratory corridors used may be due to factors such as dietary preference, rather than species-specific environmental tolerances. By demonstrating that environmental conditions affect the migratory behaviours of marine migrants, this study suggests spatially and temporally dynamic management is required for effective long-term conservation.

Finally, in **Chapter 6**, I summarise and discuss the findings from this thesis, highlighting the importance of combining complementary methodologies to better understand the complex life histories and movements of marine migrants. I further discuss how this information can help inform dynamic management strategies to help protect this mostly elusive taxa and I propose some novel areas of future research.

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CHAPTER 2: GLOBAL REVIEW AND INVENTORY: HOW STABLE ISOTOPES ARE HELPING US UNDERSTAND ECOLOGY AND INFORM CONSERVATION OF MARINE TURTLES

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ABSTRACT

Stable isotope analysis (SIA) has become a powerful and widely utilised tool in ecological studies, and more specifically has been used to answer conservation questions regarding key marine indicator species including marine turtles. Undertaking an exhaustive review of peer-reviewed literature, we summarise the current knowledge of marine turtle spatial, foraging, and reproductive ecology gained through stable isotope studies and highlight the considerable flexibility and ecological complexities in the life histories of the six species that have been studied. We demonstrate how SIA can inform conservation initiatives, identify threats faced, and provide pre- and post-disaster information that is otherwise unavailable. We summarise isotope ratios at a global scale and demonstrate intraspecific regional differences and interspecific overlap. We identify the geographical gaps in the current knowledge and the bias in the species studied. To facilitate future research we identify a comprehensive list of recommendations including the need for standardised protocols for tissue collection and analysis, the use of a third forensic marker to provide greater power of inference, combining complementary techniques to enhance the information gained, conducting long-term research, and a need for meta-analytic approaches to combine research findings to better understand the complexities of marine turtle ecology. This review provides a complete list of all published marine turtle stable isotope studies which are summarised in an open access inventory to enable researchers to add new studies and target future work.

KEY WORDS: SIA, $\delta^{13}C$, $\delta^{15}N$, Sea turtle, Foraging ecology, Migratory connectivity, Reproductive ecology, Threats

INTRODUCTION

1.1 Background

As a group of large marine vertebrates found widely throughout the temperate and tropical oceans, marine turtles can be considered as key indicator species of ecosystem function and health. Marine turtles have complex life histories (Miller 1997, Musick & Limpus 1997, Plotkin 2003), often with multiple ontogenetic shifts in habitat and diet (e.g. Snover et al. 2008), and migrations of considerable distances between foraging and nesting grounds (e.g. James et al. 2005, Shillinger et al. 2008). Within one nesting aggregation, several geographically distinct foraging areas may be utilised and different life history strategies may be employed (e.g. Hays et al. 2006, Seminoff et al. 2008, Dujon et al. 2018). Understanding the complex life histories of marine turtles and identifying critical habitats is a research priority in marine turtle ecology (Hamann et al. 2010, Rees et al. 2016, Casale et al. 2018).

Techniques to determine the movements of these elusive species include flipper tagging (e.g. Limpus et al. 1992, Hays et al. 2010), satellite telemetry (e.g. Nichols et al. 2000, Hays et al. 2006, Jeffers & Godley 2016), and genetics (e.g. Shamblin et al. 2017). Flipper tagging requires large numbers to be tagged for successful recapture and offers no locational information between captures. Satellite telemetry is extensively used in marine turtle spatial ecology, offering detailed movement data on location and speed, however, this technique is expensive and often results in small sample sizes, limiting knowledge of population level behaviour (Godley et al. 2008). Genetics can, for example, identify connectivity between rookeries and foraging grounds but genetic studies can require broad geographic regions to be sampled (Avise 2007, Komoroske et al. 2017).

For successful conservation, it is important to protect not only the critical habitats of marine turtles but also the prey items on which they rely. Marine turtle dietary studies have historically relied on directly observing foraging behaviour (e.g. Ogden et al. 1983, Schofield et al. 2006), stomach content analysis at necropsy of stranded animals or oesophageal lavage (e.g. Seminoff et al. 2002, Santos et al. 2011), or using animal-borne cameras (e.g. Heithaus et al. 2002, Seminoff et al. 2006b, Fuller et al. 2009, Narazaki et al. 2013, Fukuoka et al. 2016, Thomson et al. 2018). Although these techniques allow for the taxonomic identification of prey items, direct observations of foraging behaviour are logistically difficult and in many cases not possible (Narazaki et al. 2013). Stomach content analysis represents a short dietary time frame and biases against rapidly digested soft-bodied prey (Duffy & Jackson 1986, Heithaus et al. 2002), whilst animal-borne camera studies are limited by adequate light, battery and storage capabilities, and generally small sample sizes (Moll et al. 2007, Narazaki et al. 2013).

1.2 Stable Isotope Analysis

Stable isotope analysis (SIA) can be a powerful tool that can complement the aforementioned methods that evaluate foraging ecology and habitat use. SIA has been used in ecological studies for a range of marine taxa that are of conservation concern (Rubenstein & Hobson 2004), including marine mammals (e.g. Newsome et al. 2010), elasmobranchs (e.g. Shiffman et al. 2012, Bird et al. 2018), and seabirds (e.g. Forero & Hobson 2003, Roscales et al. 2011). Over the last two decades SIA has become an important tool for investigating marine turtle spatial, foraging, and reproductive ecology, highlighting ecological complexities in life history strategies and enhancing conservation approaches (e.g. Ceriani et al. 2017, Reich et al. 2017, Burgett et al. 2018). The isotopes of an element have different atomic weights, which react at differing rates. This leads to natural isotope gradients in environmental & biological systems. SIA relies on measuring these isotope ratios. The ratio of stable isotopes in low-metabolically active tissue of an individual closely relates to the food it has consumed and the geographical location where it was ingested (DeNiro & Epstein 1978, 1981). Most commonly, the ratios of ^{13}C:^{12}C (expressed as $\delta^{13}C$) and ^{15}N:^{14}N (expressed as $\delta^{15}N$) are used as geographic markers resultant from variations in nutrient cycling within the water experienced by the individual (Graham et al. 2010).

The isotope ratio itself represents a time-integrated diet (Peterson & Fry 1987), can be conducted on all life stages, and the analysis is cost effective (approximately £9-15 per sample dependent on the element to be analysed), allowing for large sample sizes. Different tissue types have different residence times; for example, blood serum has a short half-life and therefore represents food consumed recently, whilst epidermis has a longer half-life and therefore represents the diet consumed several months prior (Reich et al. 2008). Therefore, by assessing different tissue types, assessment of diet at multiple time points can be conducted (e.g. Petitet & Bugoni 2017, Turner Tomaszewicz et al. 2017b).

Carbon isotope ratios reflect the primary producer responsible for the energy flow in the food chain (DeNiro & Epstein 1978, Hobson 1987). Productive benthic and nearshore regions supported by algae and seagrass exhibit higher $\delta^{13}C$ values in comparison to less productive pelagic and oceanic regions supported by phytoplankton (DeNiro & Epstein 1978, Graham et al. 2010).

With regards to phytoplankton-driven food webs, temperature primarily drives the geographical and temporal variation of $\delta^{13}C$ values, especially at higher latitudes, due to its influence on CO_2 uptake rates, dissolved CO_2 concentrations, and phytoplankton growth rates and community composition (Goericke & Fry 1994, Hinga et al. 1994, Gruber et al. 1999, Graham et al. 2010, Magozzi et al. 2017). Phytoplankton shape, size, and species influences isotopic fractionation and results in regional-scale differences in $\delta^{13}C$ values, for example between nearshore and offshore regions (Hinga et al. 1994, Pancost et al. 1997, Popp et al. 1998).

The $\delta^{15}N$ values in marine primary producers differs with (1) $\delta^{15}N$ values of their nutrient sources (e.g. nitrate, ammonium, and N_2), (2) nitrogen-based processes, including, N_2-fixation, denitrification, and nitrification, and (3) isotopic fractionation (Montoya 2007). Areas of N_2-fixation support primary producers with low $\delta^{15}N$ values as the $\delta^{15}N$ value of dissolved N_2 is near 0‰ with little isotopic fractionation during its biological uptake (Dore et al. 2002, Montoya et al. 2002, Montoya 2007). In comparison, denitrification removes ^{15}N-depleted nitrate (NO_3^-), leaving strongly ^{15}N-enriched nitrate and in turn primary producers with high $\delta^{15}N$ values (Voss et al. 2001, Dore et al. 2002). Large-scale spatial variation of phytoplankton $\delta^{15}N$ values is driven by the upwelling of ^{15}N-enriched nitrate as a result of denitrification at depth (Graham et al. 2010). Anthropogenic waste and agricultural runoff in coastal habitats increase the $\delta^{15}N$ values in particulate matter used by primary producers (Harrington et al. 1998, McKinney et al. 2002). These spatial variations are reflected in higher trophic consumers and can therefore be used as a marker for habitat use at large scales.

Nitrogen isotope ratios in individuals have also been used to reflect trophic patterns (DeNiro & Epstein 1978, 1981). It has been suggested that in marine ecosystems, a 3 to 4‰ step-wise enrichment of $\delta^{15}N$ values occurs in each subsequent trophic level as ^{15}N retention is higher than ^{14}N (Minagawa & Wada 1984, Post 2002). However, due to the many factors influencing isotope ratios this distinction is sometimes not straightforward (see Section 3.5 on limitations of this method). Previous work using compound-specific SIA (CSIA) of amino acids on marine turtles has shown variations in δ^{15}N values are due to shifts in baseline isotope ratios and not trophic position (Seminoff et al. 2012, Vander Zanden et al. 2013a, see Section 3.6 for details on CSIA).

Spatial and temporal variation in δ^{13}C and δ^{15}N values in marine phytoplankton is large, consistent and relatively well understood, to the extent that mechanistic models can capture most of the observed variance (e.g. Tagliabue & Bopp 2008, Somes et al. 2010, Schmittner & Somes 2016, Magozzi et al. 2017). These realistic predictions of baseline isotope ratios improve the interpretation of δ^{13}C and δ^{15}N values in marine organisms as geolocation tools (Graham et al. 2010, McMahon et al. 2013, Magozzi et al. 2017).

Stable isotope ratios of other elements, including sulphur (δ^{34}S) and oxygen (δ^{18}O), have also been used in marine turtle studies. δ^{34}S values differ between primary producers in sulphide-rich sediments and those with limited access to sulphide (Sullivan & Moncreiff 1990). Therefore, δ^{34}S values can be used to differentiate between ecosystems supported by seagrass and microphytobenthos, which have low δ^{34}S values, and ecosystems supported by phytoplankton and macroalage, which have high δ^{34}S values (e.g. Cardona et al. 2009, Bradshaw et al. 2017). δ^{18}O values reflect water temperature when applied to biominerals such as bones or the epifaunal barnacles on the carapace of a turtle (e.g. Killingley & Lutcavage 1983, Detjen et al. 2015).

1.3 Current review

SIA has been used in marine turtle research since 1983 (Killingley & Lutcavage 1983) and has provided an extensive range of insights into marine turtle ecology. Pearson et al. (2017) reviewed SIA data of marine turtles, but their objectives were to highlight the bias of marine turtle stable isotope studies towards populations listed by the IUCN (International Union for Conservation of Nature) as least concern.

In this review we compile the current insights into marine turtle ecology and conservation gained through SIA, highlight gaps in existing knowledge, and suggest future recommendations for the preparation and interpretation of SIA in marine turtle research. We also combine all published isotope ratios to summarise these data on a global scale. An accessible inventory of all marine turtle stable isotope research is also included to enable researchers to add new studies, target future work, and help prevent unnecessary research overlaps in the future (Table S1, see the PANGAEA data repository at doi.org/10.1594/PANGAEA.892683).

METHODOLOGY

We conducted a systematic review to determine the ecological insights gained from marine turtle stable isotope studies and determine the current gaps in this field. An extensive literature search was conducted in English (Scopus, Web of Science, and Google Scholar; last accessed 31st December 2018). The terms searched were, ‘sea turtle’, ‘marine turtle’, ‘loggerhead turtle’, ‘green turtle’, ‘leatherback’, ‘hawksbill’, ‘Kemp's ridley’, ‘olive ridley’, ‘flatback’, and ‘isotope’ in TITLE-ABSTRACT-KEYWORDS for Scopus and TOPIC for Web of Science. The top 200 papers in Google Scholar were ranked by relevance and suitable literature was selected. All peer-reviewed primary research papers were included in the analysis excluding fossil isotope studies.

From each study, isotope ratios were extracted either (1) directly from text, (2) from supplemental raw values, (3) from the range provided, (4) from a graph that provided a mean, or (5) from a scatter plot, in which case the mid-value from the range was determined by eye. Additional information including the location of the study, tissue type utilised, life stage, species, and methodology was extracted (see Table S1 for details on information collated). If life stage was unknown it was not included in the interspecies and ocean basin isotope ratio comparisons (see Sections 3.2.2 and 3.2.3). If multiple tissue-types were sampled for an individual only the epidermal isotope ratio was selected to be included in the analysis. Samples from the Atlantic Ocean were further separated into the main Atlantic basin, Gulf of Mexico, Caribbean Sea, or subtropical Northwest Atlantic (SNWA) due to previously published differences in isotope ratios attributed to the spatial variation of isotope ratios at the base of the food web rather than dietary differences (Pajuelo et al. 2012b, Vander Zanden et al. 2013a, 2015, 2016, Tucker et al. 2014, Ceriani et al. 2017). For example, nutrient-rich waters and denitrification in the Gulf of Mexico could cause higher $\delta^{15}N$ values in this region compared to the SNWA and Caribbean Sea, which is influenced by nitrogen fixation (Vander Zanden et al. 2015). The SNWA had high $\delta^{13}C$ values, which was suggested to be due to being a seagrass-dominated ecosystem compared to other regions likely supported by phytoplankton, macroalgae, and mangroves (Vander

Zanden et al. 2015). Therefore, these regions are represented separately within our analysis.

Our search results identified 114 published studies (46 since 2015) that investigated stable isotopes in marine turtles. The primary focus of 21 of these studies was on methodology whilst the remaining 93 were ecological studies (Table S1). Five methodological-based studies on captive individuals likely provided artefactual isotope ratios and were not included for geographic comparisons, however for completeness details on these studies are available in Table S1.

RESULTS AND DISCUSSION

Overview of studies

Compiling global isotope studies highlights gaps in current knowledge with a bias towards studying certain species and regions (Fig. 1 and Table 1). Loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*) are the most studied whilst, as yet, there has been no published study on flatback turtles (*Natator depressus*). Split by ocean basin Fig. 1 shows that most studies were conducted in the Atlantic (55%), followed by the Pacific (25%), Mediterranean (10%), and Indian Ocean (10%).

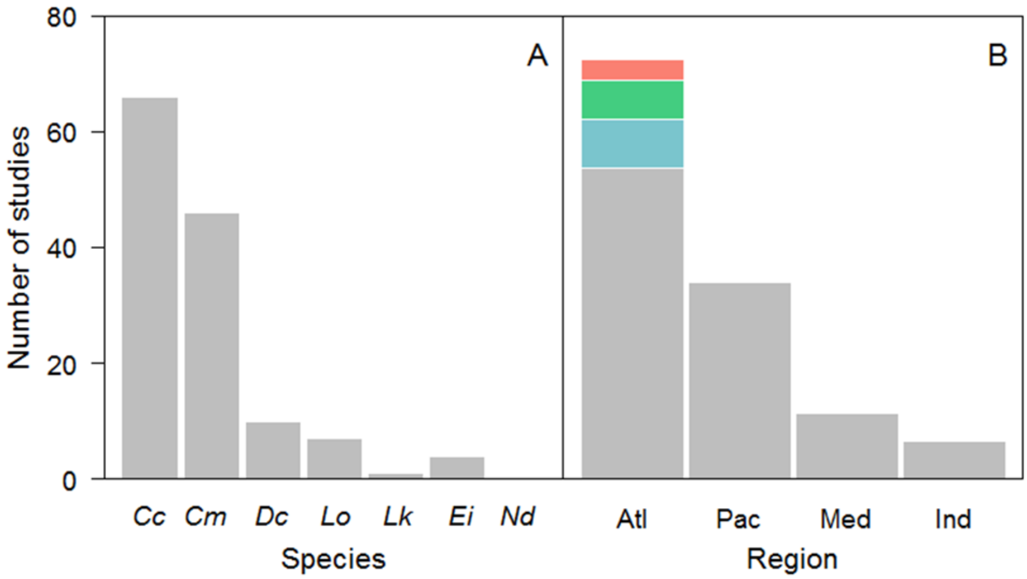

Fig. 1. Number of studies of stable isotopes in marine turtles by (A) species and (B) region. (A) *Cc*: loggerhead turtle; *Cm*: green turtle; *Dc*: leatherback turtle; *Lo*: olive ridley turtle; *Lk*: Kemp's ridley turtle; *Ei*: hawksbill turtle; *Nd*: flatback turtle. (B) Atl: Atlantic Ocean (including subtropical Northwest Atlantic [red], Caribbean Sea [green] and Gulf of Mexico [blue]); Pac: Pacific Ocean; Med: Mediterranean Sea; Ind: Indian Ocean

Mapping the location of studies globally illustrates that there are large geographical gaps in marine turtle isotope research (Fig. 2), with 77% of studies carried out in six countries (USA = 47%, Japan = 10%, Spain = 6%, Australia = 6%, Brazil = 6%, Mexico = 3%). This geographical bias is unsurprising as current SIA research is conducted on well-studied populations, and some areas of a species range are inaccessible, especially species' with restricted nesting habitats e.g. flatback turtles.

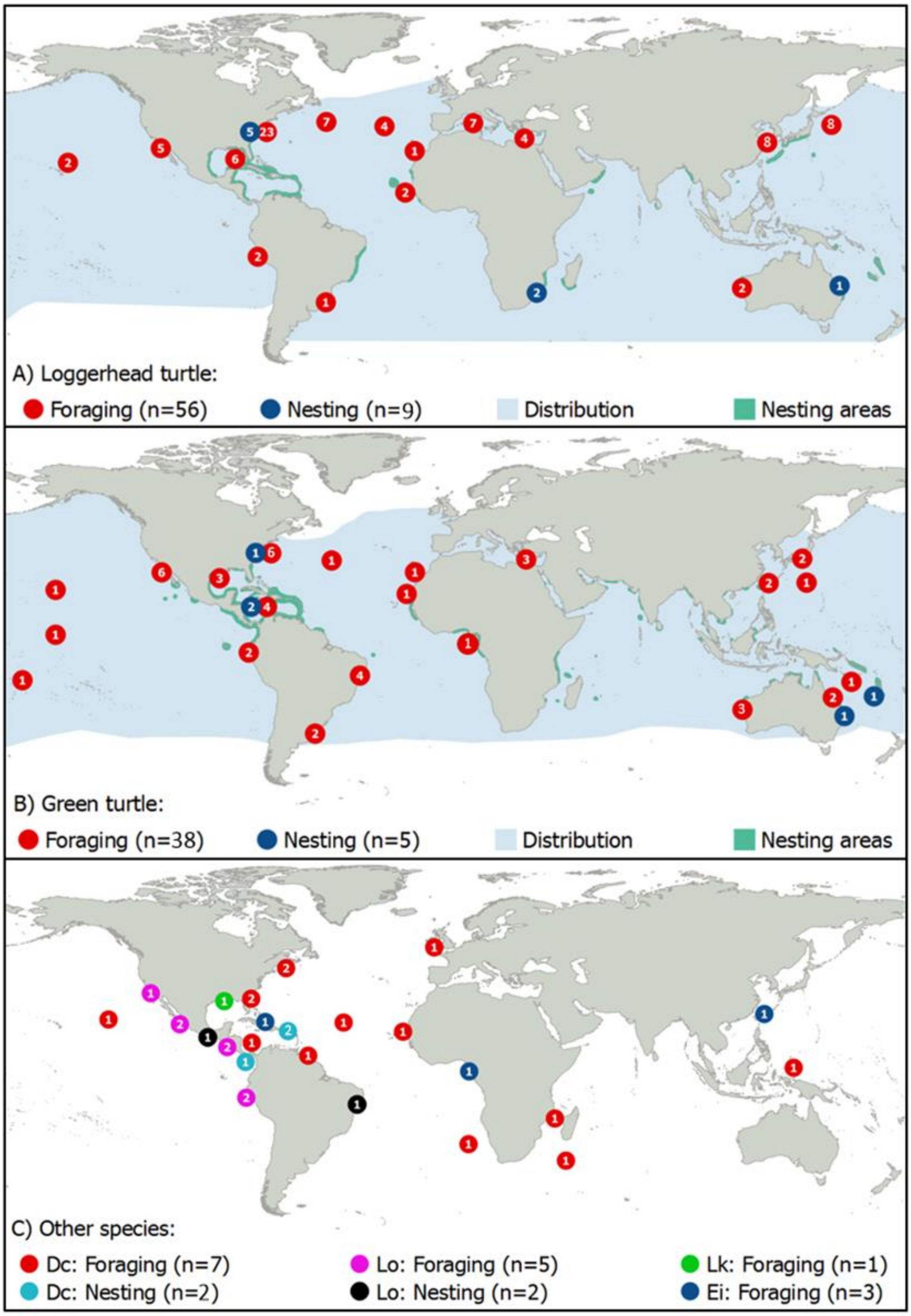

Fig. 2. Geographical location of studies investigating stable isotopes in marine turtles: (A) Loggerhead, (B) green, and (C) other species. For species abbreviations see Fig 1. Points represent studies that investigated marine turtle isotope ratios from known foraging grounds or at nesting grounds when foraging grounds were not identified. Numbers within the points represent the number of studies. Loggerhead and green turtle distributions (blue) and nesting areas (green) are shown. Distributions adapted from IUCN and nesting areas from OBIS-Seamap

Table 1. Summary of the ecological information gained from marine turtle stable isotope studies. *Cc*: loggerhead turtle; *Cm*: green turtle; *Dc*: leatherback turtle; *Lo*: olive ridley turtle; *Lk*: Kemp's ridley turtle; *Ei*: hawksbill turtle; *Nd*: flatback turtle; Pac: Pacific Ocean; Atl: Atlantic Ocean; Ind: Indian Ocean; Med: Mediterranean Sea; GoM: Gulf of Mexico; Car: Caribbean Sea; dash (-): no published studies available

	Species							**Region**						
FORAGING & SPATIAL ECOLOGY	*Cc*	*Cm*	*Dc*	*Lo*	*Lk*	*Ei*	*Nd*	Pac	Atl	Ind	Med	GoM	Car	Source
Diet	14	24	5	3	-	-	-	9	20	6	7	3	1	Godley et al. 1998, Hatase et al. 2002, 2006, Revelles et al. 2007a, b, Cardona et al. 2009, 2010, 2012, 2015, Wallace et al. 2009,2014, , McClellan et al. 2010, Vander Zanden et al. 2010, 2013a, b, 2016, Burkholder et al. 2011, Dodge et al. 2011, Lemons et al. 2011, Belicka et al. 2012, Seminoff et al. 2012, Thomson et al. 2012, 2018, Arthur et al. 2014, González Carman et al. 2014, Shimada et al. 2014, Williams et al. 2014, Bezerra et al. 2015, Goodman Hall et al. 2015, Howell et al. 2016, Prior et al. 2016, Robinson et al. 2016, Vélez-Rubio et al. 2016, Di Beneditto et al. 2017, Peavey et al. 2017, Petitet & Bugoni 2017, Sampson et al. 2017, Blasi et al. 2018, Burgett et al. 2018, Gillis et al. 2018, Hancock et al. 2018, Hetherington et al. 2018, Monzón-Argüello et al. 2018, Turner Tomaszewicz et al. 2018
Interspecies differences	8	9	2	-	-	3	-	1	6	1	2	1	1	Godley et al. 1998, Biasatti 2004, Wallace et al. 2006, Hannan et al. 2007, Reich et al. 2007, Bjorndal & Bolten 2010, Cardona et al. 2010, Agusa et al. 2011, Belicka et al. 2012, López-Castro et al. 2013, 2014a, Arthur et al. 2014, Robinson et al. 2016, Monzón-Argüello et al. 2018
Regional differences	6	1	2	-	-	-	-	2	9	-	-	6	1	Wallace et al. 2006, Pajuelo et al. 2010,2012b, Vander Zanden et al. 2013a, 2015, 2016, Tucker et al. 2014, Ceriani et al. 2017, Hetherington et al. 2018
Ontogenetic shifts	9	13	1	-	-	1	-	4	19	-	1	2	2	Reich et al. 2007, Arthur et al. 2008, Cardona et al. 2009, 2010, 2017, Snover et al. 2010, Eder et al. 2012, Avens et al. 2013, López-Castro et al. 2013, 2014a,b, González Carman et al. 2014, Shimada et al. 2014, Wallace et al. 2014, Goodman Hall et al. 2015, Ramirez et al. 2015, Howell et al. 2016, Vélez-Rubio et al. 2016, 2018, Di Beneditto et al. 2017, Turner Tomaszewicz et al. 2017a, 2018, Burgett et al. 2018, Ferreira et al. 2018, Monzón-Argüello et al. 2018
Migratory connectivity	22	9	4	2	1	-	-	12	18	2	4	6	3	Killingley & Lutcavage 1983, Hatase et al. 2006, 2010, 2013, 2014, 2015, 2018, Reich et al. 2010, 2017, Dodge et al. 2011, Watanabe et al. 2011, Zbinden et al. 2011, Ceriani et al. 2012, 2014a, 2015, 2017, Eder et al. 2012, Pajuelo et al. 2012a, b, Seminoff et al. 2012, Thomson et al. 2012, López-Castro et al. 2013, 2014a, Vander

														Zanden et al. 2013a, 2014a, 2015, Cardona et al. 2014, 2017, Wallace et al. 2014, Detjen et al. 2015, Prior et al. 2016, Robinson et al. 2016, Bradshaw et al. 2017, Madigan et al. 2017, Peavey et al. 2017, Price et al. 2017, Turner Tomaszewicz et al. 2018, Vélez-Rubio et al. 2018
Foraging site fidelity	13	5	2	-	-	-	-	5	12	2	1	3	1	Hatase et al. 2002, 2013, Vander Zanden et al. 2010, 2013b, 2014a, 2016; Eder et al. 2012, Pajuelo et al. 2012b, 2016, Seminoff et al. 2012, Thomson et al. 2012, Kaufman et al. 2014, Shimada et al. 2014, Tucker et al. 2014, Goodman Hall et al. 2015, Prior et al. 2016, Robinson et al. 2016, Bradshaw et al. 2017, Cardona et al. 2017, Vélez-Rubio et al. 2018
Foraging dichotomy	11	1	3	-	-	-	-	10	2	2	1	-	0	Hatase et al. 2002, 2006, 2010, 2013, 2014, 2015, 2018, Caut et al. 2008b, Watanabe et al. 2011, Zbinden et al. 2011, Eder et al. 2012, Seminoff et al. 2012, Robinson et al. 2016, Cardona et al. 2017, Hatase & Omuta 2018
SIZE, GROWTH AND REPRODUCTIVE OUTPUT														
Growth	9	9	-	-	-	3	-	6	11	-	3	1	-	Hatase et al. 2002, 2010, Revelles et al. 2007a, Cardona et al. 2009, Wallace et al. 2009, Bjorndal & Bolten 2010, Pajuelo et al. 2010, Agusa et al. 2011, Allen et al. 2013, Williams et al. 2014, Goodman Hall et al. 2015, Clusa et al. 2016, Vélez-Rubio et al. 2016, 2018, Di Beneditto et al. 2017, Blasi et al. 2018, Burgett et al. 2018, Ferreira et al. 2018, Monzón-Argüello et al. 2018, Turner Tomaszewicz et al. 2018
Adult size	20	4	1	1	-	-	-	11	10	2	2	3	-	Godley et al. 1998, Hatase et al. 2002, 2006, 2010, 2013, 2014, 2015, 2018, Reich et al. 2010, Burkholder et al. 2011, Watanabe et al. 2011, Zbinden et al. 2011, Pajuelo et al. 2012b, 2016, Thomson et al. 2012, Ceriani et al. 2014a, 2015, Tucker et al. 2014, Vander Zanden et al. 2014a, Wallace et al. 2014, Carpentier et al. 2015, Prior et al. 2016, Cardona et al. 2017, Peavey et al. 2017, Price et al. 2017
Reproductive output	12	-	1	-	-	-	-	6	5	-	2	2	-	Caut et al. 2008b, Hatase et al. 2010, 2013, 2014, 2015, 2018, Zbinden et al. 2011, Eder et al. 2012, Cardona et al. 2014, Vander Zanden et al. 2014a, Ceriani et al. 2015, 2017, Hatase & Omuta 2018, Hetherington et al. 2018
THREATS	9	7	-	3	1	1	-	7	7	1	3	2	-	Hannan et al. 2007, Revelles et al. 2007a, Caut et al. 2008a, Wallace et al. 2009, Páez-Osuna et al. 2010, Agusa et al. 2011, Lemons et al. 2011, Allen et al. 2013, Ceriani et al. 2014a, Bezerra et al. 2015, Clusa et al. 2016, Vander Zanden et al. 2016, Le Gouvello et al. 2017, Madigan et al. 2017, Petitet & Bugoni 2017, Reich et al. 2017, Blasi et al. 2018, Monzón-Argüello et al. 2018, Turner Tomaszewicz et al. 2018

We show that adult females were sampled most frequently (44%, including studies that sampled hatchlings and eggs as a proxy for maternal tissue), followed by juveniles (40%), and adult males (16%; Table S2 in the Supplement). A large range of tissue types have been sampled with epidermis sampled the most frequently (30%), followed by scute (carapace, 15.5%), egg yolk (9%), red blood cells (9%), humeri (7.5%), blood plasma (7%), muscle (6%), whole blood (6%), whole egg (albumen and yolk, 2%), blood serum (2%), albumen (1%), egg shell (1%), embryos (1%), epibionts (1%), liver (1%), and tendon (1%).

These findings support the review by Pearson et al. (2017), who suggest that the focus of future work should be directed at under-studied species, for example flatback turtles, and we suggest more needs to be done globally across the full range and life stages of all species. Information on habitat use is highly useful for all populations, particularly those less studied or those in highly disturbed areas.

3.2 Foraging and spatial ecology

Summarising marine turtle stable isotope studies demonstrated that the majority (83%) have investigated foraging ecology specifics, including identifying foraging grounds, foraging site fidelity, and diet (Table 1). This is also the case for marine mammal and elasmobranch ecology where SIA is most commonly used to study diet and trophic position (Forero & Hobson 2003, Newsome et al. 2010, Shiffman et al. 2012). Understanding the variation in foraging strategies enables population-level questions to be answered, for example, individual variations in life history strategies and carry-over effects between foraging and breeding seasons (e.g. Caut et al. 2008b, Ceriani et al. 2017, Hatase et al. 2018). SIA also enables the demographic trends of a population to be better understood (e.g. Bradshaw et al. 2017) and the threats faced by a population (both environmental and anthropogenic) to be assessed (e.g. Clusa et al. 2016, Vander Zanden et al. 2016).

3.2.1 Diet

The proportion of prey items contributing to the diet of an individual can be estimated from their isotope ratio via isotope mixing models. See Section 3.6 for details and limitations of mixing models. This is a major area of study in marine turtle research and has enabled the diet of several marine turtle populations to be estimated, showing the large variability in intra- and inter-species diets (Table 1). Isotope studies of adult and juvenile loggerhead turtles in neritic foraging grounds have shown that the dominant prey were benthic items such as molluscs and crustaceans (Hatase et al. 2002, Wallace et al. 2009, McClellan et al. 2010, Goodman Hall et al. 2015) whilst the dominant prey for individuals in oceanic foraging grounds were pelagic prey, for example macroplankton, including gelatinous zooplankton and jellyfish (Hatase et al. 2002, Revelles et al. 2007b, McClellan et al. 2010, Cardona et al. 2012).

Depending on the population, within neritic foraging grounds, adult and juvenile green turtles were suggested to consume macrophytes (Bezerra et al. 2015, Howell et al. 2016, Prior et al. 2016, Di Beneditto et al. 2017). However, SIA has shown the presence, and in some cases dominance, of animal-based matter demonstrating omnivorous behaviour (Godley et al. 1998, Hatase et al. 2006, Cardona et al. 2009, 2010, Burkholder et al. 2011, Lemons et al. 2011, Belicka et al. 2012, González Carman et al. 2014, Shimada et al. 2014, Williams et al. 2014, Vélez-Rubio et al. 2016, Sampson et al. 2017, Burgett et al. 2018, Gillis et al. 2018, Hancock et al. 2018, Monzón-Argüello et al. 2018, Thomson et al. 2018, Turner Tomaszewicz et al. 2018). There is also evidence that adult green turtles forage from the water column in coastal regions (Turner Tomaszewicz et al. 2018) and on macroplankton in oceanic regions (Hatase et al. 2006) foragers.

Isotopes can also be used to infer both individual specialisation and the ecological niche of a species based on the intra- and inter-individual variation in isotope ratios (Newsome et al. 2007, Vander Zanden et al. 2010, 2013b, 2016, Burkholder et al. 2011, Lemons et al. 2011, Ferreira et al. 2018, Thomson et al. 2018). To estimate individual consistency and specialisation, analysis of variance techniques have been used (e.g. Vander Zanden et al. 2010, 2013b, 2016, Lemons et al. 2011), whilst to estimate isotopic niche width studies have used the Layman et al. (2007) total area metric (e.g. Burkholder et al. 2011) or Stable Isotope Bayesian Ellipses in R (SIBER, Jackson et al. 2011, e.g. Ferreira et al. 2018, Hancock et al. 2018). Using SIA, individual specialisation has been reported for other marine taxa including sharks (e.g. Matich et al. 2011) and marine mammals and penguins (e.g. Cherel et al. 2007). Understanding the diet resources used by a population enables temporal shifts to be monitored and it also informs conservation strategies allowing the targeting and management of the turtle foraging grounds and the diverse range of prey on which they rely.

3.2.2 Global interspecies differences in isotope ratios

Several studies have conducted SIA on multiple species (Table 1). For example, previous interspecies comparisons in isotope ratios showed adult loggerhead turtles had higher $\delta^{15}N$ values and in some cases lower $\delta^{13}C$ values than green turtles, suggesting higher trophic level foraging (Godley et al. 1998, Hannan et al. 2007, Monzón-Argüello et al. 2018), whilst no differences were seen between oceanic loggerhead and juvenile green turtles, suggesting similar prey items and foraging locations (Reich et al. 2007, Cardona et al. 2010, López-Castro et al. 2013). One SIA study showed that adult leatherback turtles (*Dermochelys coriacea*), differing from loggerhead and green turtles (Godley et al. 1998), have an oceanic foraging strategy, whilst a second study revealed an unexpected neritic foraging strategy of leatherback turtles in the Indian Ocean (Robinson et al. 2016).

Isotope studies have suggested minimal levels of interspecific competition in foraging resources between hawksbill (*Eretmochelys imbricate*) and green turtles in the Caribbean, with hawksbill turtles foraging at higher trophic levels (Bjorndal & Bolten 2010). However, no differences have been reported between green and hawksbill turtles in Japan (Agusa et al. 2011). These contrasting findings are likely due to dietary differences. Further analysis could be performed to estimate differences in diet composition and trophic positions within these populations using mixing models and CSIA (see Section 3.6). SIA has been used to investigate interspecies differences in isotope ratios within other marine taxonomic groups including marine mammals (e.g. Burton & Koch 1999, Newsome et al. 2010), seabirds (Forero & Hobson 2003), penguins (Cherel et al. 2007), and elasmobranchs (e.g. Shiffman et al. 2012, Bird et al. 2018).

This review combines global marine turtle isotope ratios, demonstrating that clear species differences do not occur globally, for either adults or juveniles, with large overlapping interspecies ranges (Fig. 3, Table S2). This is likely due to the many complex factors affecting isotope ratios (see Section 1.2) as well as ocean basin differences in baseline isotope ratios (see Section 3.2.3). For adults, green turtles were the most distinct species with low δ^{15}N and high δ^{13}C values. Loggerhead turtles had intermediate isotope ratios whilst hawksbill, Kemp's ridley (*Lepidochelys kempii*), leatherback, and olive ridley turtles (*Lepidochelys olivacea*) had similar mean values with high δ^{15}N and low δ^{13}C values. Within juveniles, green and hawksbill turtles had low δ^{15}N and high δ^{13}C values in comparison to the other species. Only single studies investigated adult hawksbill and Kemp's ridley turtles and juvenile leatherback and olive ridley turtles and therefore do not represent their global isotope ratios. In addition, the ratios used for these analyses stemmed from multiple tissue types that were preserved and prepared with different techniques, which can affect isotope results (see Section 3.7).

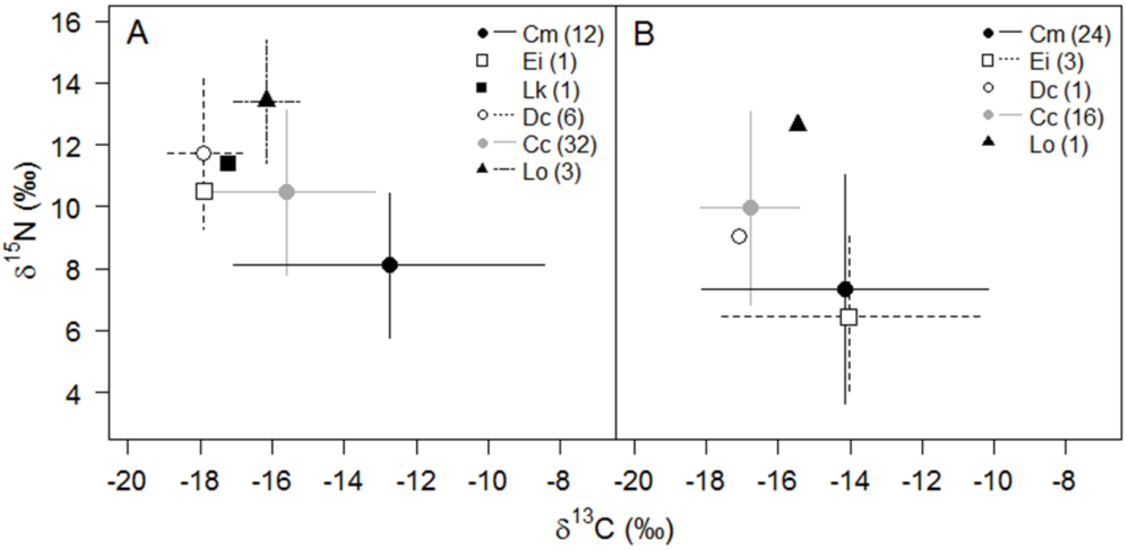

Fig. 3. Interspecific differences in stable isotope ratios in marine turtles. Mean of mean δ^{13}C and δ^{15}N across studies of (A) adult and (B) non-adult marine turtles. Mean ±SD shown where n > 1. Number of studies contributing are shown in parentheses. Non-adults include juvenile, immature, and sub-adult individuals. For species abbreviations see Fig. 1

When we further split the global data by ocean basin, different interspecies relationships are shown (Fig. S1 in the Supplement). This is unlikely due to distinct intraspecies differences in foraging strategy across ocean basins, but rather due to local variations in isotope ratios at the base of the food chain of the sampled populations.

3.2.3 Ocean basin differences in isotope ratios

The majority of studies to date focus on individual populations in specific regions, whilst few studies have investigated how a species' isotope ratios differ between ocean basins (Table 1). In this review we compiled ocean basin isotope ratios for each species and show that the large intraspecies ranges previously observed (see Section 3.2.2) are likely partly due to geographical variation (Fig. 4, Table S2; for other species plots see Fig. S2 in the Supplement). We show that adult loggerhead turtles foraging in the SNWA were the most isotopically distinct with low $\delta^{15}N$ and high $\delta^{13}C$ values. Atlantic, Gulf of Mexico, Pacific, and Mediterranean loggerhead turtles had similar ratios with high $\delta^{15}N$ and low $\delta^{13}C$ values. Considerable overlap is seen in the isotope ratios of juvenile loggerhead turtles in different ocean basins, with a relatively narrow range of $\delta^{13}C$ values in all regions compared to $\delta^{15}N$ values. Fewer values were available for green turtles. Adult green turtles had similar $\delta^{15}N$ values for all ocean basins, whilst adults from the Pacific and Indian Ocean had low $\delta^{13}C$ values in comparison to other ocean basins and the Atlantic had large ranges in isotope ratios. Isotope ratios were more distinct in juveniles, with those foraging in the SNWA showing low $\delta^{15}N$ and high $\delta^{13}C$ values whilst Atlantic and Pacific foragers had low $\delta^{13}C$ but high $\delta^{15}N$ values. Adult leatherback turtles had similar $\delta^{13}C$ values for all ocean basins, whilst adults from the Pacific had relatively high $\delta^{15}N$ values.

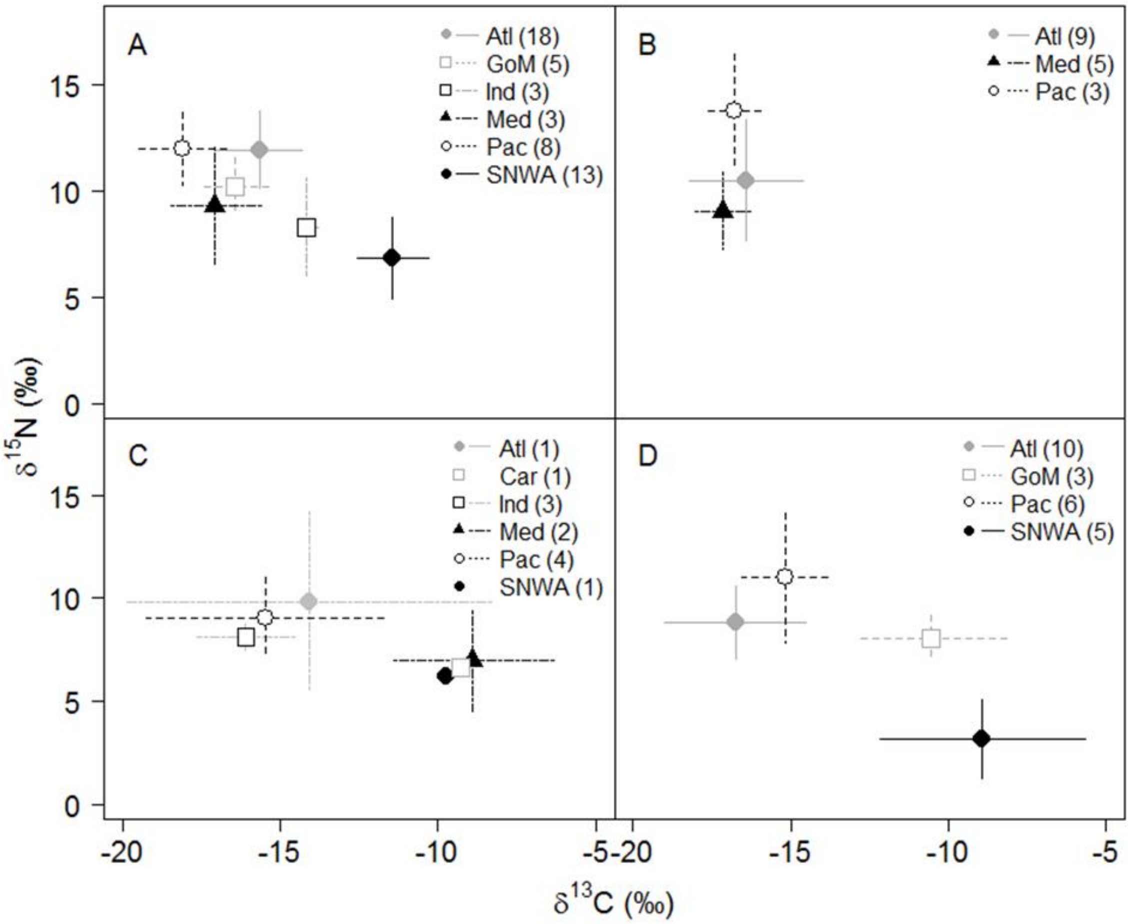

Fig. 4. Intraspecific variation of δ^{13}C and δ^{15}N values for loggerhead turtle (A) adults, (B) non-adults, and green turtle (C) adults, and (D) non-adults. Mean ±SD shown where n > 1. Number of studies contributing are shown in parentheses. Non-adults include juvenile, immature, and sub-adult individuals. Atl: Atlantic Ocean; Car: Caribbean Sea; GoM = Gulf of Mexico; Ind: Indian Ocean; Med: Mediterranean Sea; Pac: Pacific Ocean; SNWA: subtropical Northwest Atlantic

Previously published ocean basin comparisons between Pacific and Atlantic leatherback (Wallace et al. 2006) and loggerhead turtles (Pajuelo et al. 2010) demonstrated those in the Pacific had higher δ^{15}N values. High δ^{13}C and low δ^{15}N values have been reported in the SNWA and Caribbean Sea compared to the Gulf of Mexico and east coast USA for loggerhead and green turtles (Pajuelo et al. 2012b, Vander Zanden et al. 2013a, 2015, 2016, Tucker et al. 2014, Ceriani et al. 2017). Global variations in isotope ratios can be seen in previously created marine isoscapes (e.g. Somes et al. 2010, Magozzi et al. 2017, Bird et al. 2018), and we suggest intraspecies variations between ocean basin are due to dissimilarities in local and ocean basin nutrient cycling regimes that influence isotope ratios at the base of the food web, which in turn influence the ratios of higher trophic level consumers. It is essential that when comparing isotope values from multiple regions, researchers quantify the baseline isotope ratios or obtain a proxy for the baseline ratios, for example from previous studies on lower trophic level species, amino acid δ^{15}N values, or isoscapes (maps of the geospatial distribution of isotopes).

3.2.4 Ontogenetic shifts

The geographical location of marine turtle developmental stages and the movement between developmental areas are relatively unknown, as satellite telemetry of these life stages is limited (Godley et al. 2008). This is important information for conservation, as threats in these regions are less understood and in turn protection measures for this developmental life stage are limited (Hamann et al. 2010). Many studies have used isotopes to investigate ontogenetic shifts (Table 1).

SIA has revealed that ontogenetic shifts are facultative not obligatory, depending on whether a habitat meets the demands of an individual (Hatase et al. 2006) and can be either over a year or over several years (e.g. Reich et al. 2007, Cardona et al. 2009, 2010, González Carman et al. 2014, López-Castro et al. 2014b, Ramirez et al. 2015, 2017, Vélez-Rubio et al. 2016, Di Beneditto et al. 2017). Such analysis can also allow researchers to calculate the age and size at which a marine turtle ontogenetic shift occurs (e.g. Snover et al. 2010, Avens et al. 2013, Ramirez et al. 2015, 2017, Howell et al. 2016, Turner Tomaszewicz et al. 2017a, 2018, Vélez-Rubio et al. 2018) and in turn estimate the duration of each life stage and the subsequent threats faced, which can be used to better understand and model population dynamics.

3.2.5 Migratory connectivity

To date, nesting beaches remain the main target for conservation action; however, as the terrestrial proportion of the life cycle of marine turtles is so brief, prioritising the conservation of important marine habitats and identifying the geospatial linkages within a population should be a priority. From nesting beaches, inaccessible foraging grounds and migratory connectivity can be identified using SIA (Table 1). To represent foraging grounds, tissues with slow turnover rates of months (e.g. epidermis) should be sampled (see Section 3.7 for recommendations on the tissue type to sample). By compiling all studies to date, we show the majority sampled foraging grounds (38%, either by directed capture for research or using animals caught in fisheries), followed by nesting grounds (35%), strandings (26.5%), and/or mating grounds (0.5%).

Quantifying the baseline isotope ratios in a region can be useful for interpreting marine turtle foraging and migratory behaviour. Several models have provided realistic predictions of global baseline isotope ratios (e.g. Tagliabue & Bopp 2008, Somes et al. 2010, Schmittner & Somes 2016, Magozzi et al. 2017) and a few isoscapes are available for the open ocean (e.g. Graham et al. 2010, McMahon et al. 2013). However, these show the geographical gradients of isotopes at very coarse resolutions. Recently, isoscapes have been developed for coastal and shelf areas (e.g. Vander Zanden et al. 2015, Trueman et al. 2017). SIA can be used in combination with satellite telemetry to identify foraging grounds with distinct isotope ratios and in turn assign individuals to putative foraging grounds. This has become common practice in marine turtle ecology, with the majority of studies that sampled nesting grounds proceeding to assign individuals to putative foraging grounds (60%). This enables dispersion of adult females to be estimated with reasonable certainty. SIA can also be used to identify potential foraging grounds with distinct isotope ratios, even when these foraging grounds have not been previously identified via satellite telemetry. These can then be further investigated with targeted satellite tracking of individuals to identify the location of the foraging ground associated with the distinct isotope ratios (e.g. Bradshaw et al. 2017).

Once the foraging grounds of a population have been identified, the relative importance of each foraging ground can be estimated by calculating the proportion of females supported by each area (e.g. Hatase et al. 2010, 2013, Reich et al. 2010, Zbinden et al. 2011, Eder et al. 2012, Cardona et al. 2014, Vander Zanden et al. 2014a, Ceriani et al. 2015, 2017, Bradshaw et al. 2017, Price et al. 2017). Differences in the growth and reproductive output of each foraging ground can also be assessed and used as another method of determining the relative importance of a foraging ground (see Section 3.3). Long-term multi-year studies enable the contributions to annual nesting cohorts and recruitment to be estimated and therefore to identify foraging ground dynamics and in turn demographic trends of the population (e.g. Pajuelo et al. 2012a, Vander Zanden et al. 2014a, Ceriani et al. 2015, 2017, Bradshaw et al. 2017, Price et al. 2017). This baseline information could then be used to target conservation efforts of more threatened and/or important foraging grounds.

In comparison to adult females, males are greatly underrepresented in stable isotope studies due to accessibility difficulties. Males should be prioritised for study, as the current dataset is not large enough to provide a solid conclusion on differences in isotope ratios between male and female marine turtles. Using SIA, adult males were suggested to forage in similar regions as females (Pajuelo et al. 2012b) and to forage on similar prey as no differences were observed in the isotope ratios of male and female loggerhead (Thomson et al. 2012, Pajuelo et al. 2012a), green (Vander Zanden et al. 2013a, Prior et al. 2016), or olive ridley turtles (Peavey et al. 2017). Sex differences in isotope ratios were not observed in leatherback turtles when epidermis was sampled (Dodge et al. 2011, Wallace et al. 2014) but were observed within blood samples (whole blood and red blood cells, Dodge et al. 2011). Wallace et al. (2014) suggest the difference in findings between these studies is likely due to differences in incorporation rates among tissue types sampled, but could be due to between-sex foraging differences of different leatherback turtle populations. Although plasma has relatively quicker incorporation rates compared to epidermis, and therefore would explain differences in whole blood and epidermis isotope ratios, red blood cells have slow turnover rates that are similar to epidermis and thus represent similar time frames. Therefore, differences in foraging strategies may exist among leatherback turtle populations. This highlights the importance of selecting the correct tissue type for the question under investigation (see Section 3.7 for recommendations on the tissue type to sample).

3.2.6 Foraging site fidelity

To ascertain foraging site fidelity of an individual the temporal consistency of their isotope ratios is commonly used (Table 1). SIA has been used to infer foraging site fidelity in marine mammals using whale baleen to create multiyear isotopic records to show shifts in foraging ecology and habitat use (e.g. Schell et al. 1989, Newsome et al. 2010). To determine temporal consistency in isotope ratios marine turtle isotope studies have either combined skeletochronology and SIA, enabling prior diet and habitat to be reconstructed (see Section 3.6 for details on skeletochronology and SIA; e.g. Eder et al. 2012, López-Castro et al. 2013, Wallace et al. 2014, Ferreira et al. 2018), or have sampled individuals across multiple years (e.g. Thomson et al. 2012, Tucker et al. 2014, Goodman Hall et al. 2015). However, there are limitations in using SIA for identifying foraging site fidelity, as other factors such as the influence of algal blooms or small scale nutrient cycling shifts on isotope ratios may occur rather than shifts in foraging location (e.g. Tucker et al. 2014). Therefore, stable isotopes alone are not entirely sufficient in some cases, and it is important to verify SIA with satellite telemetry or a third forensic marker (see Section 3.7 for recommendations on complementary techniques).

Marine turtle isotope studies have shown that post-ontogenetic juvenile loggerhead turtles and sexually mature females exhibit long-term site and diet fidelity (Hatase et al. 2002, 2013, Vander Zanden et al. 2010, 2016, Thomson et al. 2012, Tucker et al. 2014, Goodman Hall et al. 2015, Cardona et al. 2017). A study of male loggerhead turtles suggested the level of behavioural plasticity depends on the foraging ground used (Pajuelo et al. 2012b, 2016), showing SIA can be used to identify sex differences in life history strategies.

Eder et al. (2012) conducted SIA on the outer section of humeri from loggerhead turtles in Cape Verde and used skeletochronology to age the turtles. They found neritic loggerhead turtles in Cape Verde were older than adult oceanic foragers and suggested that females moved to more neritic regions, with increasing age suggesting foraging ground shifts can occur in later years. However, a later study on the same population by Cardona et al. (2017) analysed the isotope ratios from different layers of inert carapace and showed no isotopic differences. The latter study therefore suggested, instead of shifting habitat as reported by Eder et al. (2012), it was more likely that this population exhibits long-term site fidelity and that oceanic foragers had a shorter life expectancy (see Section 3.3 for more details on the carry-over effects of foraging grounds). This highlights how SIA results can be incorrectly interpreted and the importance of combining complementary techniques (see Section 3.7 for recommendations on complementary techniques).

Isotope-based studies examining the extent of site fidelity in adult green turtles found high foraging site fidelity (Shimada et al. 2014, Vander Zanden et al. 2013b, Bradshaw et al. 2017) whilst a study by Prior et al. (2016) demonstrates a common shift between foraging grounds. Prior et al. (2016) analysed two tissue types (epidermis and blood serum) which have different turnover rates (long and short, respectively) with isotope ratios of blood serum showing short-term shifts in habitat use, whilst those showing foraging site fidelity used only one tissue type with slow turnover rates (scute or epidermis). This highlights that certain sampling methods have associated limitations on temporal detail, and this should be considered when interpreting results.

High site fidelity and individual specialisation could indicate limited adaptability to changes in foraging grounds and it is possible some individuals remain in sub-optimal foraging regions, which could have subsequent carry-over effects (see Section 3.3 for more details on the carry-over effects of foraging grounds).

3.2.7 Foraging dichotomies

Regardless of species, marine turtle hatchlings are considered omnivores that later switch to a more specialised diet. However, stable isotope studies have demonstrated the system is more complex. Nesting populations are not simply composed of females foraging in several similar foraging grounds with a specialised diet, but that in some cases a distinct foraging dichotomy occurs, for example with females foraging neritically or oceanically (Table 1). In general, adult loggerhead and green turtles were previously considered exclusive neritic foragers whilst leatherback turtles were thought of as oceanic foragers (Bjorndal 1997). Stable isotopes have revealed foraging dichotomy between oceanic and neritic foraging grounds for all three species (Hatase et al. 2002, 2006, Caut et al. 2008b, Watanabe et al. 2011, Eder et al. 2012, Cardona et al. 2017). Different foraging strategies will lead to exposure of different threats and environmental conditions and therefore conservation strategies must take this into consideration. Using SIA, different foraging strategies (oceanic vs. neritic) within a species have been highlighted in marine mammal research (e.g. Walker et al. 1999). Reich et al. (2010) proposed a nearshore-offshore foraging dichotomy for NWA loggerheads based on isotope ratios, however, this study did not use satellite telemetry whilst later studies using SIA and satellite telemetry suggested the isotopic difference is, in fact, more likely due to a latitudinal gradient (e.g. Ceriani et al. 2012, Pajuelo et al. 2012a). This highlights the importance of supporting SIA results with satellite telemetry (see Section 3.7 for recommendations on complementary techniques).

Foraging dichotomies represent dramatic life history differences within a population. For example, neritic loggerhead turtles are typically larger than their oceanic conspecifics, a difference in size that has been attributed to the nutritional benefits of neritic prey (Hatase et al. 2002, 2010, 2013, 2014, 2015, 2018, Watanabe et al. 2011, Eder et al. 2012, Cardona et al. 2017). Combing SIA and genetics, Watanabe et al. (2011) found nesting populations demonstrating foraging dichotomies were genetically homogeneous, suggesting that size-related foraging dichotomy may be due to phenotypic plasticity and that foraging habitats do not affect offspring morphology (Hatase et al. 2015, 2018). No size difference was observed between neritic and oceanic female green turtles suggesting the nutritional benefits of their main prey did not differ (Hatase et al. 2006). Difference in reproductive output has however been reported between individuals with different foraging strategies (see Section 3.3.3).

3.3 Size, growth and reproductive output

In addition to foraging and spatial ecology, marine turtle stable isotope studies have begun to elucidate the complexities of marine turtle reproductive ecology and other life history traits (Table 1). Carry-over effects, the influence of one activity (e.g. foraging) on another (e.g. breeding), will likely differ among foraging grounds and foraging strategies affecting fitness correlates (Harrison et al. 2011). As marine turtles generally show philopatry to foraging sites, carry-over effects could last longer than one remigration cycle.

3.3.1 Juvenile size and growth

Differences in turtle body size have been observed between foraging grounds in juvenile loggerhead turtles (Allen et al. 2013, Clusa et al. 2016) but not green turtles (Di Beneditto et al. 2017). Hatase et al. (2002) suggested that immature loggerhead turtles recruited to nutrient-rich benthic habitats will grow larger than those recruited to nutrient-low pelagic habitats, but will reach sexual maturity at a similar age (Hatase et al. 2010). Revelles et al. (2007a) found no difference in juvenile loggerhead turtle size between neritic and oceanic individuals; however, they also found the isotope ratios of prey items did not differ, suggesting all juveniles were foraging pelagically irrespective of water depth.

Many studies investigate the direct relationship between size and δ^{15}N and/or δ^{13}C values to infer the occurrence of ontogenetic shifts (e.g. Cardona et al. 2009, Goodman Hall et al. 2015, Vélez-Rubio et al. 2016, 2018, Burgett et al. 2018, Monzón-Argüello et al. 2018), diet (e.g. Wallace et al. 2009, Williams et al. 2014, Blasi et al. 2018, Ferreira et al. 2018), habitat differences (Bjorndal & Bolten 2010), foraging site fidelity (e.g. Goodman Hall et al. 2015, Monzón-Argüello et al. 2018, Turner Tomaszewicz et al. 2018), age-at-maturity (e.g. Turner Tomaszewicz et al. 2018), and threats faced (e.g. Agusa et al. 2011, Clusa et al. 2016). These studies reported different relationships between juvenile size and δ^{15}N and/or δ^{13}C values for loggerhead, green, and hawksbill turtles, suggesting difference in life history traits between populations. However, caution should be taken when interpreting isotope ratios in this regards, as incorporation rates and trophic discrimination factors (TDFs) can be influenced by body size and growth (see Section 3.5 for details on this limitation).

3.3.2 Adult size and growth

Morphological differences in female body size, are a known factor affecting reproductive output (Bjorndal & Carr 1989, Broderick et al. 2003) and therefore size differences between foraging strategies could influence reproductive fitness. Morphological differences in size have been seen between foraging grounds for females (Zbinden et al. 2011, Ceriani et al. 2014a, 2015, Vander Zanden et al. 2014a, Price et al. 2017) but not males (although small samples sizes were reported for these; Pajuelo et al. 2012b, 2016). As with juveniles, the direct relationship between δ^{15}N and/or δ^{13}C values and female size, regardless of foraging ground, is dependent on the species or population studied (Godley et al. 1998, Hatase et al. 2002, Burkholder et al. 2011, Eder et al. 2012, Thomson et al. 2012, Tucker et al. 2014, Wallace et al. 2014, Carpentier et al. 2015, Prior et al. 2016, Peavey et al. 2017). For sharks, δ^{13}C values were not seen to differ with size for neritic or oceanic species; however, size did affect the isotope ratio of deep-sea sharks (at depths >200m) suggesting their trophic ecology is size-structured (Bird et al. 2018).

3.3.3 Reproductive output

The allocation of resources to reproductive traits may differ between foraging grounds and may result in trade-offs between life history parameters. When female size is accounted for, foraging ground also affects loggerhead turtle clutch size. SIA and satellite telemetry have been used to identify foraging dichotomies within nesting populations and have been used to assign females to either neritic or oceanic foraging grounds (e.g. Hatase et al. 2002, 2006, Caut et al. 2008b, Watanabe et al. 2011, Eder et al. 2012, Cardona et al. 2017; see Section 3.2.7 for details on these studies). In turn, SIA studies have used this information to show females foraging in neritic regions had larger clutches and clutch volumes than their oceanic conspecifics (Eder et al. 2012, Hatase et al. 2013, 2015, 2018), whilst no difference was seen in egg size, nutritional components, hatchling size, or nest site selection between neritic and oceanic foragers, suggesting trade-offs between clutch size and egg quality do not occur (Hatase et al. 2014, 2015, 2018, Hatase & Omuta 2018). In addition, studies investigating the isotopes of nesting females from populations only foraging in neritic regions found differences in clutch size were still evident between foraging grounds (Zbinden et al. 2011, Cardona et al. 2014, Ceriani et al. 2015, 2017) showing both foraging strategy and foraging location can cause carry-over effects.

Foraging ground did not affect loggerhead turtle hatchling production, as measured by the number of hatchlings that emerged from an individual nest, in populations exhibiting foraging dichotomy (Hatase et al. 2013, 2015, 2018) or between neritic foraging grounds in the Northwest Atlantic (NWA; Vander Zanden et al. 2014a, Ceriani et al. 2015). However, a latter study of the NWA loggerhead turtles found there was a difference in hatchling production between foraging grounds (Ceriani et al. 2017). This inconsistency was not discussed in Ceriani et al. (2017), however, Ceriani et al. (2017) isotopically assigned females to more foraging regions than previous studies and used a continuous-surface approach that, they stated, was an improvement on previous assignment models allowing for the inclusion of all sampled individuals. This highlights the importance of identifying all foraging grounds utilised by a population and how analytical developments can improve the interpretation of isotope ratios.

Remigration interval (the number of years between breeding events) is dependent on the quality and quantity of resources at the foraging ground, as individuals require energy reserves for migration, vitellogenesis, and nesting (e.g. Saba et al. 2007). Foraging ground has been seen to affect the remigration interval of loggerhead turtles (Vander Zanden et al. 2014a, Ceriani et al. 2015); in particular, those isotopically assigned to neritic foraging regions had shorter remigration intervals than those foraging in oceanic regions, which could lead to higher reproductive output (Hatase et al. 2013). This was also observed for leatherback turtles (Caut et al. 2008b), whilst Hetherington et al. (2018) suggested oceanographic conditions (North Atlantic Oscillation) may influence leatherback turtle nesting parameters with low North Atlantic Oscillation values linked with low $\delta^{15}N$ values, longer remigration intervals, and lower clutch frequency.

Female loggerhead turtles assigned to neritic foraging grounds, in comparison to their oceanic conspecifics, had higher clutch frequency (number of clutches in a season), breeding frequency (number of nesting seasons) and in turn cumulative reproductive output with more emergent hatchlings (Hatase et al. 2013). Clutch frequency varied more for neritic foragers than oceanic foragers and was attributed to shifts in prey availability (Hatase et al. 2013). Individuals from neritic-only foraging grounds were interpreted as having slight differences in arrival date (Vander Zanden et al. 2014a), which can affect the temperature of incubation and in turn the sex ratio (Wibbels 2003). No differences were seen for individuals isotopically assigned to foraging grounds in the number of clutches laid (Vander Zanden et al. 2014a), duration of the nesting season (Vander Zanden et al. 2014a), breeding lifespan (period from first to last nesting season) (Hatase et al. 2013), age at sexual maturity (Hatase et al. 2010), incubation duration (Hatase et al. 2015, 2018), survival (Hatase et al. 2013), or hatchling righting response (Hatase et al. 2018).

3.4 Applications of SIA for management and conservation

In addition to the conservation insights afforded by enhancing the understanding of ecology, stable isotope studies have been used to identify and better contextualise threats faced by marine turtles. One of the earliest applications of SIA was for wildlife forensics to determine the origin of 'tortoiseshell' for the management of the illegal trade of turtle products (Moncada et al. 1997). SIA has been used successfully to aid the policing of African elephant (*Loxodonta africana*) ivory (Vogel et al. 1990) and could be used for reptile populations e.g. crocodile lizards (*Shinisaurus crocodilurus*) (van Schingen et al. 2016). Moncada et al. (1997) analysed $\delta^{13}C$ and $\delta^{15}N$ values and showed no distinct difference in the isotope ratio of ranched versus wild hawksbill turtles. Within this review we have highlighted the difficulty of distinguishing marine turtle species based on $\delta^{13}C$ and $\delta^{15}N$ values (see Section 3.2.2); therefore, analysis of additional elements or alternative forensic markers is required for wildlife forensics to successfully identify the origin of marine turtle products.

As a result of foraging site fidelity, SIA of inert tissue has the potential to provide pre- and post-disaster information that is often unavailable and has shown individuals appear to remain in foraging grounds even after devastating anthropogenic activities. For example, after the *Deepwater Horizon* disaster in 2010, turtles in the Gulf of Mexico continued to forage in oil- and chemical dispersant-affected areas (Vander Zanden et al. 2016, Reich et al. 2017), resulting in the potential incorporation of pollutants and a slowing of the growth of the population (Reich et al. 2017).

The incorporation of contaminants offers a possible practical application in the use of toxicological proxies as additional forensic markers to help further separate foraging regions in marine mammal (e.g. Born et al. 2003, Krahn et al. 2008) and shark studies (Shiffman et al. 2012) and could be utilised further in future marine turtle isotope research. SIA has been used in marine turtle ecotoxicology studies to show the presence of pollutants in marine turtles, including the increase of persistent organic pollutants in green turtles fed fish and cephalopods by divers (Monzón-Argüello et al. 2018). SIA has also been used to show the effect of provisioning for ecotourism in elasmobranchs (e.g. Maljković & Côté 2011) and the impact of consuming fishery discards on fish (e.g. Boyle et al. 2012) and seabirds (e.g. Forero & Hobson 2003, Bugoni et al. 2010). SIA has helped reveal highly elevated mercury levels in green turtles foraging close to industrial activities despite foraging on the same prey as individuals foraging in non-industrial areas (Bezerra et al. 2015). Bioaccumulation of arsenic and arsenic compounds was observed in green and hawksbill turtles with the latter more carnivorous species, as demonstrated by SIA, exhibiting heavier loading (Agusa et al. 2011). The presence of Fukushima-derived radiocesium in olive ridley turtles (Madigan et al. 2017), and low maternal transfer of lead (attributed to non-anthropogenic sources) in nesting olive ridley females has been assessed using SIA (Páez-Osuna et al. 2010). Biomagnification of pollutants up through trophic levels has also been assessed using SIA in marine mammals and seabirds (e.g. Forero & Hobson 2003, Tomy et al. 2004, Newsome et al. 2010).

Isotope studies have enabled interactions with fisheries to be identified, including the consumption of fishery discards by green (Turner Tomaszewicz et al. 2018) and olive ridley turtles (Petitet & Bugoni 2017), potential ingestion by loggerhead turtles of fish and squid from baited long-line hooks, which poses a potential bycatch threat (Revelles et al. 2007a, Blasi et al. 2018), and juvenile loggerhead turtles foraging food commonly bycaught or purposefully caught which could increase competitive interactions (Wallace et al. 2009). Previous SIA work has found the size and genetic stock of turtles bycaught is based on fishing region not fishing gear, which can help target conservation (Clusa et al. 2016). Isotope ratios revealed olive ridley turtles foraged in neritic and oceanic grounds showing they can encounter both longline and trawl fisheries, which is of concern (Petitet & Bugoni 2017), and that loggerhead turtles caught in California drift gillnets are likely those that normally forage in the central North Pacific, which are incidentally caught in the Hawaii-based longline fishery (Allen et al. 2013).

Stable isotope studies have also shown predation of marine turtle hatchlings by black rats (*Rattus rattus*) during the offseason for seabird nesting (Caut et al. 2008a) and the importance of turtle eggs as a nutrient input to the beach ecosystem aiding in dune and beach stabilisation (Hannan et al. 2007, Le Gouvello et al. 2017).

3.5 Limitations of SIA

With technological and statistical advancements, the strength of SIA is ever-increasing. However, there are still many limitations to this tool, which should be considered in future studies and understood when reading the current SIA literature. For detailed reviews on the limitations of SIA in ecology see Martínez del Rio et al. (2009) and Wolf et al. (2009). Here we summarize the major limitations and caveats of using SIA in marine turtle ecology.

Temporal variations in the stable isotope ratios at the base of the food chain can occur, for example seasonal fluctuations of zooplankton isotope ratios

(Hannides et al. 2009). This is likely due to temporal changes in the physicochemical and biological composition of the primary producers (Ramos & González-Solís 2012). This variability will be transferred up the food chain, putting in to question the seasonal stability of stable isotopes and isoscapes, which are relied on to trace predator movements (Graham et al. 2010, Ramos & González-Solís 2012). For example, seasonal differences observed by Tucker et al. (2014) for loggerhead turtles in the Gulf of Mexico were due to baseline changes in isotope ratios, which were exhibited up the food chain, rather than seasonal habitat shifts of the turtles. This can limit the use of SIA in assignment studies and highlights the importance of using complementary satellite tracking to confirm the foraging site fidelity of a population.

Newsome et al. (2010) describe in detail why isotope ratios may shift during fasting and periods of nutritional stress in marine mammals and may explain why isotope ratios of marine turtles could shift across a nesting season due to fasting, migratory foraging, inter-nesting foraging, or a consequence of egg formation (e.g. Hatase et al. 2006, Caut et al. 2008b, Zbinden et al. 2011, Petitet & Bugoni 2017). We therefore recommend samples be taken from breeding individuals as early in the season as possible to best represent the foraging ground.

The time frame represented by each tissue type is dependent on the metabolic turnover rate of that tissue (Reich et al. 2008). Isotopic turnover rates can vary with body size, growth rate, diet quality, and protein turnover (for details, see review by Wolf et al. 2009). Known turnover rates of tissues are important but lacking in large marine taxa, such as marine turtles, seabirds (Forero & Hobson 2003), marine mammals (Newsome et al. 2010), and elasmobranchs (Shiffman et al. 2012) due to the limited ability to perform diet-switching experiments. Therefore, the time frames that tissue-types represent are not well known despite being required to accurately interpret SIA results and should be carefully considered when designing future ecological studies (Ramos & González-Solís 2012).

Inherent variation of stable isotopes (isotope differences between consumers due to differences in their physiology, not diet) are often overlooked in marine turtle SIA studies, and instead the variation in isotope ratios between individuals is related to differences in diet or habitat. To estimate dietary or habitat effects on the stable isotope composition of a population with greater confidence, the amount of inherent variation within the population needs to be estimated but this information is sparse in ecology studies (Barnes et al. 2008), and the marine turtle literature is no exception. Vander Zanden et al. (2012) found that a small portion of the isotopic variation measured in a wild green turtle population was due to inherent variation, whilst the majority of variation resulted from diet and/or habitat differences. Similar values of inherent variation were reported for juvenile green turtles by Seminoff et al. (2006a), whilst Seminoff et al. (2009) found juvenile leatherbacks had larger inherent variation (for comparison between these studies, see Vander Zanden et al. 2012). As inherent variation can differ with species, life stage, and tissue (Barnes et al. 2008, Vander Zanden et al. 2012), additional studies are required for marine turtles, and Barnes et al. (2008) suggests inherent variation should be quantified on a case-by-case basis.

Trophic discrimination factors (TDFs) are the difference between predator and prey isotope ratios (represented as $\Delta = \delta_{\text{tissue}} - \delta_{\text{diet}}$) and are used in SIA literature to infer relative trophic positions and for dietary reconstructions. However, a clear understanding of TDFs is critical to prevent the incorrect interpretation of isotope ratios and incorrect outputs for mixing models (Post 2002, Caut et al. 2009, Martínez del Rio et al. 2009, Wolf et al. 2009).

Many studies use generalised diet-tissue discrimination factors such as 3-4‰ for nitrogen and 0-1‰ for carbon (Post 2002) as species-specific TDFs are limited (Caut et al. 2009). This is because they require studies of captive individuals fed on a consistent diet for sufficient time, which is difficult especially for large marine vertebrates such as marine turtles (Turner Tomaszewicz et al. 2017b). There are only a few TDFs available for marine mammals (Newsome et al. 2010), and elasmobranchs (Shiffman et al. 2012). See Newsome et al. (2010) for review of TDFs in marine mammals. TDFs are limited for marine turtles but have been estimated for several tissues types, life stages, and species, including juvenile and adult green turtles (Seminoff et al. 2006a, Vander Zanden et al. 2012, Turner Tomaszewicz et al. 2017b), hatchling and juvenile loggerhead turtles (Reich et al. 2008) and juvenile leatherback turtles (Seminoff et al. 2009); however, these are often based on small sample sizes. Differences were observed between the TDFs calculated for juvenile green turtles by Seminoff et al. (2006a) compared to those calculated by Vander Zanden et al. (2012) and Turner Tomaszewicz et al. (2017b). This difference was attributed to differences in diet, growth rates, and lipid extraction and highlights the sensitivity of TDFs.

The majority of these study animals were fed pelleted diets, whilst future experimental studies should ideally use the same food sources the consumers would encounter in the wild (Healy et al. 2018, Caut et al. 2009). These species-specific TDFs have been used by other marine turtle studies even when sampling different populations, life stages, or tissue (e.g. Burgett et al. 2018, Gillis et al. 2018, Monzón-Argüello et al. 2018).

When discrimination factors cannot be measured experimentally, Caut et al. (2009) propose a way of estimating the TDF of a consumer (the Diet-Dependent Discrimination Factor method); however, this only provides a mean TDF that can then be included in isotope mixing models (see Section 3.6 for details on isotope mixing models). A new analytical approach to estimate TDFs has been developed, the R package SIDER (Healy et al. 2018), which calculates the TDF of a consumer based on their ecology and phylogenetic relatedness. The estimated TDF and the associated uncertainty can then be included in mixing models. However, this R package is not yet applicable to reptiles.

There are also new Bayesian techniques to estimate the trophic position of a consumer, for example, the R package tRophicPosition (Quezada-Romegialli et al. 2018). This approach estimates the trophic position of a consumer at a population level using the consumer and baseline stable isotope ratios, whilst taking into account inherent variation within the population and sampling errors for TDFs and baseline and consumer isotope ratios (Quezada-Romegialli et al. 2018). One limitation of this method is that TDFs are incorporated into the model as raw data and Quezada-Romegialli et al. (2018) suggest the selection of a representative TDF is critical. Additionally, there are empirical ways to estimate trophic position, for example using compound-specific SIA (CSIA) of amino acids, which are discussed in Section 3.6.

Many studies suggest TDFs are an important area for future methodological work, however, we recommend treating the concept of TDFs with caution, as the processes that influence TDFs are not fully understood and they are likely highly dynamic, with incorporation rates of intrinsic markers into tissues differing not only with species but with sex, life stage, isotope analysed, isotopic routing, growth rates, tissue sampled, health, diet isotopic composition, and diet quality (e.g. Seminoff et al. 2006a, Reich et al. 2008, Vander Zanden et al. 2012, Turner Tomaszewicz et al. 2017b).

Martínez del Rio et al. (2009) and Wolf et al. (2009) highlight that there are far more observational field studies applying SIA than there are experimental studies aiming to understand the mechanisms behind stable isotopes and SIA, and suggest field data be accompanied by laboratory experiments. We support this recommendation and suggest the important limitations overviewed here should be considered during the design of future marine turtle studies and should be understood when reading SIA literature. Despite these limitations, SIA is undoubtedly an invaluable tool for marine turtle ecology.

3.6 Additional analytical approaches

Throughout the SIA literature, complementary techniques are often used to offer further insights about marine turtle ecology, including satellite telemetry, genetics, and stomach content analysis (as discussed in Section 1.1). Other tools used in SIA research include skeletochronology, CSIA, and mixing models. As these will likely become more common in the SIA literature, we offer a brief overview of these techniques.

Many marine turtle SIA studies sample mineralised tissues such as scutes and humeri as the isotope ratios of these chemically inert accretionary tissues do not change after formation (Snover et al. 2010). Skeletochronology specifically relates to analysing skeletal growth increments, which in marine turtle research is usually sampled from humeri. SIA of inert tissues enables a time-series of the prior diet and habitat to be reconstructed from different layers of the accretionary tissue, showing either seasonal or inter-annual changes. This technique is often used to infer life history patterns, for example the occurrence of ontogenetic shifts (e.g. Ramirez et al. 2017, Turner Tomaszewicz et al. 2017a), or to track movements (e.g. López-Castro et al. 2013, Vander Zanden et al. 2015). Marine mammal isotope studies have analysed accretionary tissues such as teeth to show dietary shifts, differences in maternal strategies, as well as ontogenetic shifts (Newsome et al. 2009, 2010). One limitation of this technique is understanding the species-specific growth rates and turnover rates and therefore the time frame each tissue layer represents, and this is recommended for future experimental work (Pajuelo et al. 2016). The periodicity of bone growth layers have, however, been validated for several marine turtle species (Snover et al. 2007, 2010). Another limitation of sampling scute is that unlike bone, scute tissue only represents a short time-series of 0.8 to 2 years (Vander Zanden et al. 2013b). Turner Tomaszewicz et al. (2017a) highlight the likely time delay between prey consumption and the assimilation into inert accretionary tissues, which may prevent a detailed estimation of the ontogenetic shift, especially in the most recent tissue layers. In addition, samples from humeri can only be obtained from dead turtles during necropsies, whilst scute samples can be obtained non-invasively depending on the depth of sample required.

CSIA can provide additional and in many cases more detailed information to bulk tissue SIA helping minimize assumptions related to the interpretation of bulk tissue isotope ratios (see review by Evershed et al. 2007). Stable isotopes of specific organic molecules, e.g. fatty acids and amino acids, have only been analysed in a few marine turtle studies (e.g. Belicka et al. 2012, Cardona et al. 2015) but are likely to be used more frequently in the future.

Fatty acid fingerprinting and amino acid analysis can be important techniques in diet studies aiming to trace the source of organic matter in food webs and the relative abundance of prey items within a diet (Belicka et al. 2012). In some cases, SIA alone cannot differentiate between primary sources of organic matter (seagrass, epiphytes, macroalgae) and therefore, might over- or under-emphasise their importance within diets (Jaschinski et al. 2008, Crawley et al. 2009, Larsen et al. 2012). Taxon-specific fatty acids are produced by phytoplankton, microzooplankton, and bacteria which are deposited into consumer adipose tissue with minimal modification and are therefore reflected within the consumers (Iverson et al. 2004, Budge et al. 2006). This enables fatty acid fingerprinting to estimate the source of organic matter at the base of a consumer’s food chain (Ramos & González-Solís 2012).

Fatty acid fingerprinting in combination with SIA has been used to estimate the contribution of primary producers to green and loggerhead turtle diets in Shark Bay, Australia (Belicka et al. 2012). However, this study suggested large sample sizes are required to separate these primary producers further. Belicka et al. (2012) also suggest fatty acid fingerprinting should be used with caution for green turtles, as hindgut bacterial fermentation could cause considerable modifications of fatty acids prior to deposition in lipid reserves (Seaborn et al. 2005). Higher trophic prey items can also be distinguished within marine turtle diets, for example the contribution of sardines and anchovies to marine turtle diet (e.g. Cardona et al. 2015). Fatty acid isotopes are considered more specific to the dietary source compared to bulk stable isotopes; whilst physiology could influence fatty acid isotope ratios of consumers. This was not considered to be the case for green and loggerhead turtles (Cardona et al. 2015). De Troch et al. (2012) highlight the importance of considering bioconversion of fatty acids when using them as biomarkers, as it is possible they undergo degradation and transformation through the food chain. Fatty acids also only makeup a small proportion of the total organic carbon, whilst amino acids account for a large proportion of organic carbon and nitrogen, and therefore amino acid analysis is considered more representative of the diet as a whole (Hedges et al. 2001).

Essential amino acids (EAAs) produced at the base of the food chain have distinct isotope ratios (i.e. $\delta^{13}C_{EAA}$) and due to little to no isotopic fractionation up the food chain can be used as intrinsic markers in high trophic consumers (O'Brien et al. 2002, Larsen et al. 2009, 2012, 2013). In addition, bulk $\delta^{13}C$ values at the base of the food chain can be influenced by variable environmental conditions (affecting growth rates and cell surface area) whilst $\delta^{13}C_{EAA}$ does not appear to be affected by environmental conditions (Larsen et al. 2013). However, as with fatty acids, hindgut fermentation performed by hindgut microflora in consumers, e.g. green turtles, might influence $\delta^{13}C_{EAA}$. EAAs have been used to explore the influence of marine turtle gut microflora on $\delta^{13}C_{EAA}$. By analysing $\delta^{13}C_{EAA}$ in herbivorous green turtle tissue, Arthur et al. (2014) found that individuals receive a large contribution of EAAs from a bacterial source, whilst EAAs of carnivorous green, loggerhead, and olive ridley turtles were from microalgae sources in oceanic food webs. EAAs could therefore be used to differentiate between herbivores and carnivores; however, it does not differentiate whether the bacterial source of $\delta^{13}C_{EAA}$ is from gut microflora or epiphytes in the food. Further analysis (linear discriminant analysis) was required to show the $\delta^{13}C_{EAA}$ indeed stemmed from gut microflora (Arthur et al. 2014).

A limitation of SIA is the inability to decipher whether differences in bulk $\delta^{15}N$ values are due to baseline isotope shifts or the influence of the trophic position of the consumer. CSIA of amino acids can determine if differences in bulk $\delta^{15}N$ values are due to differences in 'trophic' amino acids (e.g. glutamic acid and alanine), which reflect trophic level, or 'source' amino acids (e.g. phenylalanine and lysine), which reflect isotope composition of the primary producers at the base of the food chain (McClelland & Montoya 2002). This enables trophic position to be estimated without sampling prey items (Seminoff et al. 2012) and has been used to show that differences in bulk δ^{15}N values were due to baseline shifts, instead of differences in trophic position for leatherback (Seminoff et al. 2012, Hetherington et al. 2018), green (Vander Zanden et al. 2013a), and olive ridley turtles (Peavey et al. 2017), which could have been misinterpreted using bulk SIA alone.

Amino acid analysis has been recommended for use in future marine mammal research to help disentangle spatial and trophic difference in isotope ratios; however, Newsome et al. (2010) state that controlled feeding studies are required to confirm the distinction between source and trophic amino acids. Peavey et al. (2017) recommend that amino acid-specific incorporation rates and trophic discrimination factors need to be better understood for different marine turtle species and tissue types. Larsen et al. (2012) highlight two limitations of amino acid analysis. Firstly, primary producers could contribute to the diet of a consumer and not be reflected in the amino acids as amino acids are not equivalent to the entire diet, and secondly, isotopic differences in amino acids between the diet and a consumer has been seen in some consumers, especially those with protein-poor diets.

CSIA of fatty acids and amino acids is complicated by the complex food chains used by marine turtles, especially carnivorous species, the diet of which will likely be based on a range of primary producers (Arthur et al. 2014). Arthur et al. (2014) discuss the potential power of analysing the isotopes of specific compounds compared to bulk tissue analysis, but highlight the need for controlled studies to validate their interpretation, which is also recommended by Larsen et al. (2012). As with any analytical tool, CSIA has considerable cost in terms of analysis time and expense, which can limit sample size (e.g. Vander Zanden et al. 2013a) and has to be considered in study design.

In marine turtle research, mixing models are used to estimate the proportional contribution of dietary items to the diet of a consumer (e.g. McClellan et al. 2010, Burgett et al. 2018, Gillis et al. 2018, Monzón-Argüello et al. 2018). Within the field of isotope ecology, common analytical tools used are mixing models, such as linear mixing models like IsoSource (Phillips & Gregg 2003), or Bayesian mixing models like SIAR (Stable Isotope Analysis in R; Parnell et al. 2010), MixSIR (Moore & Semmens 2008), and MixSIAR (Stock & Semmens 2016). IsoSource calculates a range of possible dietary contributions that could result in the consumer isotope ratio and is a very common tool used in SIA due to its ease of use, public availability, and the limited input data required; however, model outputs are often misinterpreted (Layman et al. 2012). Bayesian mixing models suggest the most likely proportional contribution of sources to consumers as these use additional *a priori* knowledge (e.g. proportional contributions of sources and potential variability in all input parameters; Layman et al. 2012). Although more advanced than IsoSource, Bayesian mixing models have high data requirements and are still sensitive to the quality of input values (for further details on mixing models and their limitations, see review by Layman et al. 2012).

There are numerous conceptual and methodological issues surrounding the use of SIA in diet reconstruction, especially using mixing models (Martínez del Rio et al. 2009, Wolf et al. 2009). To build a mixing model TDFs and incorporation rates are required for the specific tissue, life stage, and species being analysed. As discussed in Section 3.5 these are limited for marine turtles. For best results, all prey items must be included and sampled on the same time frame as the consumer tissue is synthesised (Layman et al. 2012). Sampson et al. (2017) were unable to successfully run a MixSIAR for green turtles due to the exclusion of important prey items that were not considered potential prey from previous oesophageal lavage sampling, and Williams et al (2014) felt they were unable to sample all prey items, preventing them running mixing models.

Dodge et al. (2011) also recommend locally sampled prey items to be used in preference to published isotope ratios, as inconsistencies in the isotope ratios of prey occur. Burgett et al. (2018) highlight the importance of including prey isotope ratios that are area-specific to prevent dramatically under- or overestimating prey proportions or trophic position. Large variation in baseline isotope ratios can make the results harder to interpret as seen for green turtles by Vélez-Rubio et al. (2016), and Layman et al. (2012) suggest that as temporal and spatial variability of source isotope ratios increase, the sampling effort must increase to represent this detail. Lack of distinct differences in isotope ratios between prey items especially within similar food groups (e.g. Shimada et al. 2014) limits the ability of mixing models to estimate the diet of a consumer (Layman et al. 2012). Bias in the detection of animal matter versus plant material might occur, as animal matter is protein-based and is incorporated directly into the tissue of the turtle (Cardona et al. 2009). Determining the proportion of prey in the diet of a population can also change depending on the mixing models used (Goodman Hall et al. 2015).

3.7 Key recommendations

This review reveals that several common recommendations have been made throughout the SIA literature, including standardised protocols for tissue collection and preservation, the use of an additional forensic marker or complementary techniques to provide greater power of inference, and compiling the isotope ratios of marine turtles at a global scale to facilitate meta-analytical approaches (Table 2). This review and inventory also leads us to emphasise the variation in methodological approaches used (see Table S1 for details on the methodology used by each study; data available at doi.org/10.1594/PANGAEA.89268). For global comparisons to be made, standardised protocols are needed; however, there are scientific reasons for choosing particular tissues and techniques for specific studies, and we understand these should be the primary methodological drivers.

Table 2. Key recommendations for future marine turtle stable isotope studies. SIA: Stable isotope analysis; CSIA: compound-specific SIA

Recommendation
Target under-studied species
Cover a larger geographical range
Target males
Collaborate for meta-analytical approaches
Use a standardised technique, e.g. store epidermis in 70% ethanol and freeze yolk samples
Use a standardised technique for each tissue type
Only collect multiple tissue types when comparing short- and long-term foraging
Use epidermal tissue for long-term information
Use unhatched egg yolk as a proxy for unobserved nesting females
Conduct more research on tissue turnover rates
Use conversion equations with caution.
Use tissue-types representing similar biochemical mechanisms and time frames
Conduct more research on discrimination factors
Use a standardised isotope mixing model
Use locally sampled prey
Know all foraging grounds of the population
Determine foraging site fidelity
Collect samples from as early in the nesting season as possible
Use a third forensic marker for greater power of inference
Combine SIA with complementary techniques, e.g. satellite telemetry and CSIA
Conduct multi-year studies so shifts in population dynamics can be documented and pre- and post-disaster information to be obtained

Isotope ratios of marine turtle tissue change with decomposition (Payo-Payo et al. 2013), therefore tissues must be preserved. However, the preservation of samples, including blood anticoagulants, have been shown to significantly affect isotope ratios (Barrow et al. 2008, Lemons et al. 2012, Kaufman et al. 2014, Carpena-Catoira et al. 2016). We recommend a standardised preservation technique should be implemented for each tissue type in future research, although we understand logistical reasons could restrict what techniques are used. This was also recommended by Newsome et al. (2010) for SIA in marine mammals.

Carpena-Catoira et al. (2016) recommend the storage of epidermis in dimethyl sulfoxide (DMSO) buffer when storage in liquid nitrogen is not possible; however, these authors only compare these two preservation methods. Barrow et al. (2008) found DMSO affects epidermis isotope ratios whilst ethanol does not. Storage of epidermis in ethanol was also the most common technique (44% of studies sampling epidermis) and therefore we recommend this preservation technique. Kaufman et al. (2014) recommend egg contents be frozen and only stored in ethanol if a freezer is unavailable. We support this recommendation, and freezing of egg contents was the most common technique (89% of studies sampling egg contents). Based on the most common techniques used we also recommend epibionts and tendons be stored in ethanol, inert tissues such as scute and humeri that do not decay to be air-dried, and freezing of muscle, blood, and liver. In addition, Lemons et al. (2012) recommend sodium heparin as the best blood anticoagulant when immediate centrifugation is not possible.

Despite using the same tissue type, there was variation in whether lipid extraction was performed or correction factors applied. In some cases, lipid extraction was found to influence isotopes and these differences were biologically relevant and therefore caution must be exercised (Kaufman et al. 2014, Carpentier et al. 2015, Medeiros et al. 2015, Bergamo et al. 2016). Many studies use the recommendation that samples with C:N > 3.5 should undergo lipid extraction (Post et al. 2007); however, Bergamo et al. (2016) showed the C:N ratio might not reliably predict the lipid content of marine turtle tissue samples. Newsome et al. (2010) recommend that all studies should report the mean C:N ratio and associated error of tissues undergoing SIA, which we support. We agree with the recommendation by Carpentier et al. (2015) that ideally samples would be analysed twice, pre- and post-extraction, but it is appreciated that this adds to time and cost of analysis, as highlighted by Kaufman et al. (2014) and Bergamo et al. (2016). For diet studies sampling prey items, we support the recommendation by Newsome et al. (2010) that prey items, especially lipid-rich prey, should be analysed pre- and post-extraction. Numerous chemical treatments were utilised in the extensive shark SIA dataset compiled by Bird et al. (2018) and the importance of tissue preservation, preparation, and lipid extraction methods have been highlighted as key analytical considerations in marine mammal (Newsome et al. 2010) and elasmobranch research (Shiffman et al. 2012), supporting the conclusion that the use of standardised protocols is important in all marine SIA applications.

Numerous tissue types are used in the field of marine turtle SIA (see Section 3.1) as well as other marine taxa including marine mammals (Newsome et al. 2010). As the tissue type used represents different time frames of dietary information (Reich et al. 2008), we recommend multiple tissue types only to be collected when comparing short and long-term foraging (e.g. Petitet & Bugoni 2017). The use of multiple tissues with different turnover rates has shown ontogenetic shifts in elasmobranchs (Shiffman et al. 2012). Newsome et al. (2010) recommend that for marine mammal SIA tissues selected for analysis should have long integration times and relatively slow turnover rates (e.g. epidermis) to prevent short-term diet affecting the overall isotope ratios. We also recommend that for long-term information, epidermal tissue, which has a turnover of months (Reich et al. 2008) is best and would allow comparisons between hatchlings, juveniles, and adults. Hatchling and egg tissue is derived from the mother and represents her isotope ratios (Frankel et al. 2012, Kaufman et al. 2014, Carpentier et al. 2015). Unhatched egg content isotope ratios are equivalent to freshly laid egg yolk (Zbinden et al. 2011, Ceriani et al. 2014b). Sampling fresh egg yolk is a lethal sampling method and should be avoided if possible. We therefore support the recommendation by Ceriani et al. (2014b) that unhatched egg yolk should be sampled as a proxy for unobserved nesting females. Sampling for SIA can be intrusive and future work should take ethical concerns into consideration and determine whether it is warranted.

Conversion equations have been developed for many tissue-tissue relationships, which enables isotope ratios to be compared (see Table S3 in the Supplement for all available conversion equations). However, many studies that provide conversion equations state that they should be used with caution, as they are often derived from small sample sizes, with low coefficient of determination values, or weak correlations. Without performing controlled laboratory feeding studies, there are numerous factors that can influence isotopic differentiation between tissues (see Section 3.5), and these are unlikely to be consistent in all cases.

Using a standardised tissue type (as recommended above) would prevent the need for conversion equations and would enable direct comparisons between studies. If conversions are required, we recommend studies use values from tissues with the same biochemical mechanism (i.e. collagen is high in ^{13}C enriched glycine and therefore collagen has higher δ^{13}C values in comparison to muscle) and they should only be done with tissue-types representing similar turn-over time frames, e.g. scute and epidermis (Petitet & Bugoni 2017), or unhatched egg content and epidermis (Ceriani et al. 2014b).

We support the recommendation by Belicka et al. (2012) and Ramos & González-Solís (2012) that future studies should use a third forensic marker to provide greater power of inference of dietary estimations and geographical assignments. Only six marine turtle studies have thus far used a third marker, either δ^{34}S (Cardona et al. 2009, Belicka et al. 2012, Tucker et al. 2014, Bradshaw et al. 2017), trace elements (López-Castro et al. 2013), or isotopes of trace elements, e.g. lead (López-Castro et al. 2014a). All of these techniques have limitations, for example climate and other conditions greatly affected the spatial and temporal variability of trace elements (Jickells et al. 2005). These limitations should be considered when designing studies and Ramos & González-Solís (2012) recommend caution when simultaneously analysing multiple markers due to the differences in how they are integrated into a consumers tissues (Bond 2010).

For a holistic understanding of marine turtle ecology, studies should, where possible, conduct concurrent complementary techniques such as stomach content analysis (e.g. Burkholder et al. 2011), satellite telemetry (e.g. Hatase et al. 2010), CSIA (e.g. Belicka et al. 2012, Peavey et al. 2017), and genetics (e.g. Watanabe et al. 2011). The need for complementary techniques is mirrored in seabird (Forero & Hobson 2003), marine mammal (Newsome et al. 2010), and shark ecological research (Bird et al. 2018). We support Newsome et al. (2010) who recommend the use of time-depth recorders as well as satellite telemetry in marine mammal research to confirm the use of isotopic data as proxies for diet and habitat use.

For a more complete meta-analysis the focus of future research should be on under-studied species and conducted globally across all species ranges. To understand a population as a whole, males should also be targeted in future studies, but we understand the difficulties of accessing males. We also recommend that, where possible, life stage and sex should be made clear in all publications. Studies over multiple years, rather than snap-shot studies, are also important to enable long-term shifts in population dynamics to be documented (e.g. Bradshaw et al. 2017, Ceriani et al. 2017). To fully understand the complexities of marine turtle ecology, data and findings should be combined at a global scale to facilitate meta-analytical approaches. This would also enable marine turtle species-specific isoscapes to be created. We encourage researchers to add their papers to the global inventory that we have initiated, by sending the appropriate data (under the specific column headings in Table S1) to the corresponding author for us to regularly update this open access global inventory. The open access means that this resource, and any future updates, will be available to all researchers, helping increase exposure of new studies, whilst also underpinning and accelerating new advances in the conservation of marine turtles.

CONCLUSIONS

This review confirms and details the wealth of ecological information gained from marine turtle stable isotope research. Clearly, large gaps in knowledge for several species and life stages exist, along with geographical bias in the distribution of studies. We have created a global inventory of published marine turtle stable isotope studies and data which can be continuously and easily revised as new data are collected. Recommendations, based on the extensive literature, are provided to guide future foci of ecology and conservation research of these important marine animals. Marine turtle stable isotope studies have helped reveal the complexity of marine turtle ecology, but we believe the full utility of stable isotopes is yet to be realised.

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Supporting Information

Table S2. Summary of marine turtle stable isotope studies including the life stage sampled and the isotope ratios by species and region. Life stage included adult females (F, including hatchlings and eggs); adult males (M); juveniles (J); or were unknown (U) Several studies investigated multiple species, sexes, and region and therefore feature more than once

	Life stage						
Species/Region	F	M	J	U	δ^{13}C	δ^{15}N	Source
Loggerhead turtle (*Caretta caretta*)							
Pacific	10	1	6	0	-20.00 to -14.70	9.92 to 17.10	Hatase et al. 2002, 2010, 2013, 2014, 2015, 2018a, Pajuelo et al. 2010, Watanabe et al. 2011, Allen et al. 2013, Arthur et al. 2014, Carpentier et al. 2015, Turner Tomaszewicz et al. 2015, 2016, Hatase & Omatu 2018
Atlantic	22	5	17	0	-20.50 to -9.00	3.10 to 16.39	Killingley & Lutcavage 1983, Hannan et al. 2007, Reich et al. 2007, 2010, Barrow et al. 2008, Wallace et al. 2009, McClellan et al. 2010, Pajuelo et al. 2010, 2012a, b, 2016, Snover et al. 2010, Vander Zanden et al. 2010, 2014a, b, 2015, 2016, Ceriani et al. 2012, 2014a, b, 2015, 2017, Eder et al. 2012, Frankel et al. 2012, Avens et al. 2013, Lopez-Castro et al. 2013, 2014, Kaufman et al. 2014, Tucker et al. 2014, Goodman Hall et al. 2015, Medeiros et al. 2015, Ramirez et al. 2015, 2017, Turner Tomaszewicz et al. 2015, Cardona et al. 2017, Price et al. 2017, Monzón-Argüello et al. 2018
Gulf of Mexico	6	1	0	0	-17.83 to -14.93	8.32 to 12.89	Ceriani et al. 2012, 2015, 2017, Pajuelo et al. 2012b, Tucker et al. 2014 Vander Zanden et al. 2015, 2016
Mediterranean	4	1	6	2	-19.25 to -15.40	6.00 to 14.00	Godley et al. 1998, Revelles et al. 2007a, b, Cardona et al. 2010, 2012, 2014, 2015, Zbinden et al. 2011, Payo-Payo et al. 2013, Clusa et al. 2016, Blasi et al. 2018
Indian	4	2	1	0	-14.50 to -13.62	6.90 to 10.95	Belicka et al. 2012, Thomson et al. 2012, Robinson et al. 2016, Le Gouvello et al. 2017
Green turtle (*Chelonia mydas*)							
Pacific	8	7	12	0	-19.00 to -9.40	6.30 to 16.90	Hatase et al. 2006, Arthur et al. 2008, 2014, Caut et al. 2008a, Agusa et al. 2011, Lemons et al. 2011, 2012, Shimada et al. 2014, Detjen et al. 2015, Turner Tomaszewicz et al. 2015, 2016, 2017b, 2018, Prior et al. 2016, Sampson et al. 2017
Caribbean	3	1	3	0	-10.00 to -9.00	5.60 to 6.60	Biasatti et al. 2004, Lopez-Castro et al. 2013, 2014, Vander Zanden et al. 2013a, b
Atlantic	5	2	21	0	-28.3 to -5.80	0.85 to 13.20	Hannan et al. 2007, Reich et al. 2007, Barrow et al. 2008, Cardona et al. 2009, Bjorndal & Bolten 2010, Lopez-Castro et al. 2013, 2014, Vander Zanden et al. 2013a, b, Gonzalez et al. 2014, Bezerra et al. 2015, Bergamo et al. 2016, Velez-Rubio et al. 2016, 2018, Di Beneditto et al. 2017, Burgett et al. 2018, Gillis et al. 2018, Hancock et al. 2018, Monzón-Argüello et al. 2018

Gulf of Mexico	0	0	5	0	-12.90 to -8.00	6.50 to 9.10	Lopez-Castro et al. 2013, 2014, Vander Zanden et al. 2013a, Williams et al. 2014, Howell et al. 2016
Mediterranean	3	1	1	0	-16.23 to -5.50	5.00 to 11.00	Godley et al. 1998, Cardona et al. 2010, Bradshaw et al. 2017
Indian	3	3	0	1	-19.50 to -11.00	6.0 to 10.0	Burkholder et al. 2011, Belicka et al. 2012, Thomson et al. 2018
Leatherback turtle (*Dermochelys coriacea*)							
Pacific	2	0	0	0	-19.00 to -16.50	11.55 to 16.10	Wallace et al. 2006, Seminoff et al. 2012
Caribbean	1	0	0	0	-12.30 to -8.40	-	Biasatti et al. 2004
Atlantic	7	3	2	0	-19.20 to -16.90	4.20 to 14.10	Godley et al. 1998, Biasatti et al. 2004, Wallace et al. 2006, 2014, Caut et al. 2008b, Dodge et al. 2011, Hetherington et al. 2018
Indian	1	0	0	0	-18.45 to -16.45	11.00 to 11.50	Robinson et al. 2016
Olive ridley turtle (*Lepidochelys olivacea*)							
Pacific	4	2	1	1	-18.10 to -15.40	11.70 to 17.00	Biasatti et al. 2004, Páez-Osuna et al. 2010, Arthur et al. 2014, Carpena-Catoira et al. 2016, Madigan et al. 2017, Peavey et al. 2017
Atlantic	1	0	0	0	-16.56	10.83	Petitet & Bugoni 2017
Kemp's ridley turtle (*Lepidochelys kempii*)							
Gulf of Mexico	1	0	0	0	-17.2	11.4	Reich et al. 2017
Hawksbill turtle (*Eretmochelys imbricata*)							
Pacific	0	0	1	0	-16.16	6.22	Agusa et al. 2011
Atlantic	1	1	2	0	-17.90 to -9.85	5.43 to 10.50	Bjorndal & Bolten 2010, Ferreira et al. 2018

Table S3. Tissue conversion equations available for all marine turtles. RBC: red blood cells; U: unhatched; Fre: fresh; Fro: frozen; LE: lipid extracted; E: ethanol

Tissue from	Tissue to	$\delta^{13}C$	r^2	*p*	$\delta^{15}N$	r^2	*p*	Sample size	Life Stage	Source
Loggerhead turtle (*Caretta caretta*)										
RBC	Epidermis	$\delta^{13}C_{epi}=0.953*\delta^{13}C_{RBC}+0.734$	0.9	-	$\delta^{15}N_{epi}=1.031*\delta^{15}N_{RBC}+1.576$	0.9	-	165	Adults	Ceriani et al. 2015
RBC	Epidermis	$\delta^{13}C_{epi}=0.8489*\delta^{13}C_{RBC}-1.6691$	0.8	<0.001	$\delta^{15}N_{epi}=0.7752*\delta^{15}N_{RBC}+3.189$	0.9	<0.001	66	Juveniles	Ceriani et al. 2014a
Whole egg (U)	RBC	$\delta^{13}C_{unhat}=0.964*\delta^{13}C_{RBC}-1.769$	0.9	<0.001	$\delta^{15}N_{unhat}=0.931*\delta^{15}N_{RBC}+3.182$	0.9	<0.001	80	Eggs/ Females	Ceriani et al. 2014b
Whole egg (U)	Epidermis	$\delta^{13}C_{unhat}=0.936*\delta^{13}C_{epi}-3.415$	0.8	<0.001	$\delta^{15}N_{unhat}=0.875*\delta^{15}N_{epi}+2.162$	0.9	<0.001	80	Eggs/Females	Ceriani et al. 2014b
Whole egg (U)	Yolk (Fre)	$\delta^{13}C_{unhat}=0.954*\delta^{13}C_{fresh}-0.935$	1	<0.001	$\delta^{15}N_{unhat}=1.001*\delta^{15}N_{fresh}+0.079$	1	<0.001	36	Eggs	Ceriani et al. 2014b
Whole egg (U)	Blood serum	$\delta^{13}C_{unhat}=0.871*\delta^{13}C_{ser}-2.564$	0.8	<0.001	$\delta^{15}N_{unhat}=0.925*\delta^{15}N_{ser}+2.348$	0.8	<0.001	36	Eggs/Females	Ceriani et al. 2014b
Yolk (Fre)	Yolk (U)	-	-	-	$\delta^{15}N_{Un}=\delta^{15}N_{Fresh}+0.49$	-	-	5	Eggs	Zbinden et al. 2011
Scute	Yolk (U)	-	0.7	0.001	$\delta^{15}N_{yolk}=0.73*\delta^{15}N_{Scute}+4.69$	0.9	<0.001	27	Females/Eggs	Zbinden et al. 2011
RBC	Epidermis	$\delta^{13}C_{epi}=1.00*\delta^{13}C_{RBC}+1.4$	1	<0.001	$\delta^{15}N_{epi}=1.12*\delta^{15}N_{RBC}+0.53$	1	<0.001	26	Males	Pajuelo et al. 2012b
Epidermis	Epidermis	$\delta^{13}C_{female}=0.51*\delta^{13}C_{hatchling}-7.38$	0.2	0.042	$\delta^{15}N_{female}=1.02*\delta^{15}N_{hatchling}-1.02$	0.9	<0.001	14	Hatchlings/Females	Frankel et al. 2012
Whole blood	Epidermis	$\delta^{13}C_{epi}=0.96*\delta^{13}C_{wholeblood}+1.98$	1	0.003	$\delta^{15}N_{epi}=0.71*\delta^{15}N_{wholeblood}+4.55$	0.8	0.054	5	Females	Carpentier et al. 2015
Whole blood	Epidermis	$\delta^{13}C_{epi}=1.01*\delta^{13}C_{wholeblood}+2.02$	1	<0.001	$\delta^{15}N_{epi}=1.08*\delta^{15}N_{wholeblood}+0.42$	0.9	<0.001	3	Hatchlings	Carpentier et al. 2015
Epidermis	Yolk (Fre)	$\delta^{13}C_{yolk}=0.89*\delta^{13}C_{epi}-5.02$	0.9	0.016	$\delta^{15}N_{yolk}=1.20*\delta^{15}N_{epi}-2.84$	0.9	0.233	5	Females/Eggs	Carpentier et al. 2015
Yolk (Fre)	Epidermis	$\delta^{13}C_{epi}=1.12*\delta^{13}C_{yolk}+6.00$	-	-	$\delta^{15}N_{epi}=0.83*\delta^{15}N_{yolk}-2.37$	-	-	5	Eggs/Females	Carpentier et al. 2015

Whole blood	Yolk (Fre)	$\delta^{13}C_{yolk}=0.90*\delta^{13}C_{wholeblood}-2.42$	1	<0.001	$\delta^{15}N_{yolk}=1.08*\delta^{15}N_{wholeblood}+0.97$	1	0.003	5	Females/Eggs	Carpentier et al. 2015
Yolk (Fre)	Whole blood	$\delta^{13}C_{wholeblood}=1.12*\delta^{13}C_{yolk}+5.62$	-	-	$\delta^{15}N_{wholeblood}=0.93*\delta^{15}N_{yolk}-0.90$	-	-	5	Eggs/Females	Carpentier et al. 2015
Epidermis	Epidermis	$\delta^{13}C_{female}=0.76*\delta^{13}C_{hatchling}-2.74$	1	0.09	-	-	-	3	Hatchlings/Females	Carpentier et al. 2015
Whole blood	Whole blood	$\delta^{13}C_{female}=1.06*\delta^{13}C_{hatchling}+1.51$	1	0.003	$\delta^{15}N_{female}=0.96*\delta^{15}N_{hatchling}-1.85$	1	0.065	3	Hatchlings/Females	Carpentier et al. 2015
Scute	Epidermis	$\delta^{13}C_{epi}=0.90*\delta^{13}C_{scute}-0.25$	0.9	<0.001	$\delta^{15}N_{epi}=0.87*\delta^{15}N_{scute}+2.41$	0.9	<0.001	33	Females	Vander Zanden et al. 2014b
Yolk (Fre/Fro)	Epidermis	$\delta^{13}C_{epi}=0.71*\delta^{13}C_{yolk}-1.86$	0.7	<0.001	$\delta^{15}N_{epi} = 1.19*\delta^{15}N_{yolk}-2.50$	0.8	<0.001	24	Eggs/Females	Kaufman et al. 2014
Yolk (Fre/Fro/LE)	Epidermis	$\delta^{13}C_{epi}=0.90* \delta^{13}C_{yolk}-0.95$	0.7	<0.001	$\delta^{15}N_{epi} = 1.05* \delta^{15}N_{yolk}-0.75$	0.8	<0.001	24	Eggs/Females	Kaufman et al. 2014
Yolk (Fre/E)	Epidermis	$\delta^{13}C_{epi}=0.58* \delta^{13}C_{yolk}-4.27$	0.5	<0.001	$\delta^{15}N_{epi} = 1.16* \delta^{15}N_{yolk}-1.90$	0.8	<0.001	24	Eggs/Females	Kaufman et al. 2014
Yolk (Fre/E/LE)	Epidermis	$\delta^{13}C_{epi}=0.91* \delta^{13}C_{yolk}-0.53$	0.5	<0.001	$\delta^{15}N_{epi} = 1.15* \delta^{15}N_{yolk}-2.04$	0.8	<0.001	24	Eggs/Females	Kaufman et al. 2014
Albumen	Epidermis	$\delta^{13}C_{epi}=0.81* \delta^{13}C_{ab}-1.73$	0.7	<0.001	$\delta^{15}N_{epi} = 0.72* \delta^{15}N_{ab}+5.55$	0.6	<0.001	61	Eggs/Females	Kaufman et al. 2014
Green turtle (*Chelonia mydas*)										
Scutes	Muscles	$\delta^{13}C_{muscle}=1.128* \delta^{13}C_{scute}+4.194$	0.9	<0.001	$\delta^{15}N_{muscle} = 1.197* \delta^{15}N_{scute}-1.095$	0.9	<0.001	12	Juveniles	Bezerra et al. 2015
Humeri	Epidermis	$\delta^{13}C_{epi}=0.54* \delta^{13}C_{humeri}-8.31$	0.2	0.01	$\delta^{15}N_{epi} = 0.89* \delta^{15}N_{humeri}+2.55$	0.6	<0.001	5	Adults and juveniles	Tomaszewicz et al. 2017b
Leatherback turtle (*Dermochelys coriacea*)										
Yolk (Fre)	Plasma	$\delta^{13}C_{plasma}=1.37* \delta^{13}C_{yolk}+4.66$	0.8	<0.001	$\delta^{15}N_{plasma} = 0.81* \delta^{15}N_{scute}+1.58$	0.9	<0.001	50	Females	Caut et al. 2008b
Yolk (Fre)	RBC	$\delta^{13}C_{RBC}=1.19* \delta^{13}C_{yolk}+3.72$	0.9	<0.001	$\delta^{15}N_{RBC} = 0.64* \delta^{15}N_{yolk}+2.76$	0.6	<0.001	50	Females	Caut et al. 2008b
Olive ridley turtle (*Lepidochelys olivacea*)										

Serum	Epidermis	$\delta^{13}C_{Epi} = 0.63* \delta^{13}C_{serum}-5.14$	0.4	-	$\delta^{15}N_{Epi} = 0.70* \delta^{15}N_{serum}+2.71$	0.9	-	39	Females	Petitet & Bugoni 2017
Serum	Scute	$\delta^{13}C_{Scute} = 1.31* \delta^{13}C_{serum}+6.10$	0.8	-	$\delta^{15}N_{Scute} = 0.81* \delta^{15}N_{serum}+0.19$	0.9	-	39	Females	Petitet & Bugoni 2017
Serum	RBC	$\delta^{13}C_{RBC} = 0.91* \delta^{13}C_{serum}+0.71$	0.7	-	$\delta^{15}N_{RBC} = 0.09* \delta^{15}N_{serum}-0.42$	1	-	39	Females	Petitet & Bugoni 2017
RBC	Epidermis	$\delta^{13}C_{Epi} = 0.70* \delta^{13}C_{RBC}-3.72$	0.6	-	$\delta^{15}N_{Epi} = 0.73* \delta^{15}N_{RBC}+3.47$	0.9	-	39	Females	Petitet & Bugoni 2017
RBC	Scute	$\delta^{13}C_{Scute} = 1.11* \delta^{13}C_{RBC}+2.68$	0.1	-	$\delta^{15}N_{Scute} = 0.83* \delta^{15}N_{serum}+1.29$	0.8	-	39	Females	Petitet & Bugoni 2017
Epidermis	Scute	$\delta^{13}C_{scute} = 0.68* \delta^{13}C_{Epi}-6.52$	0.5	-	$\delta^{15}N_{scute} = 0.94* \delta^{15}N_{Epi}-0.60$	0.8	-	39	Females	Petitet & Bugoni 2017

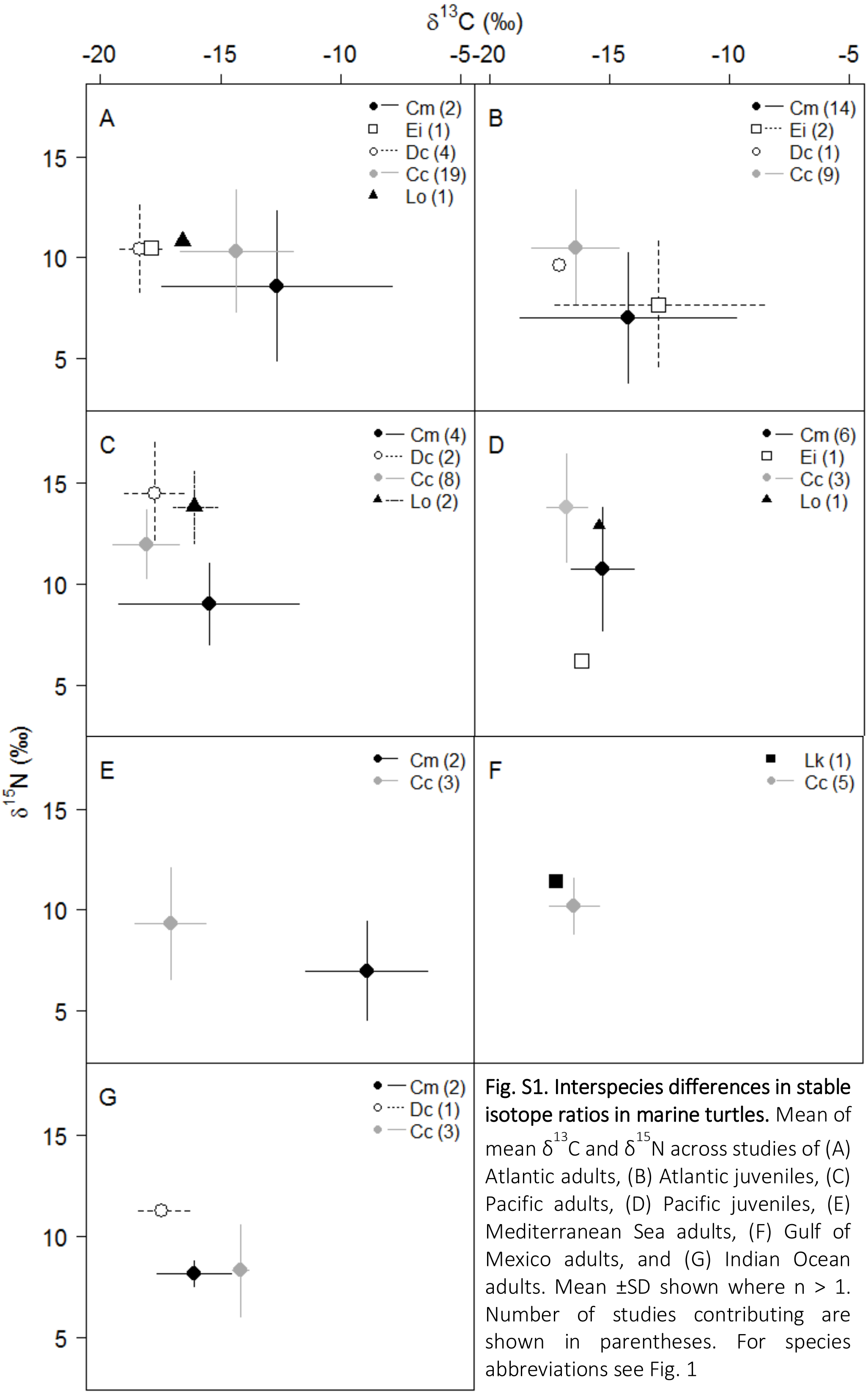

Fig. S1. Interspecies differences in stable isotope ratios in marine turtles. Mean of mean $\delta^{13}C$ and $\delta^{15}N$ across studies of (A) Atlantic adults, (B) Atlantic juveniles, (C) Pacific adults, (D) Pacific juveniles, (E) Mediterranean Sea adults, (F) Gulf of Mexico adults, and (G) Indian Ocean adults. Mean ±SD shown where n > 1. Number of studies contributing are shown in parentheses. For species abbreviations see Fig. 1

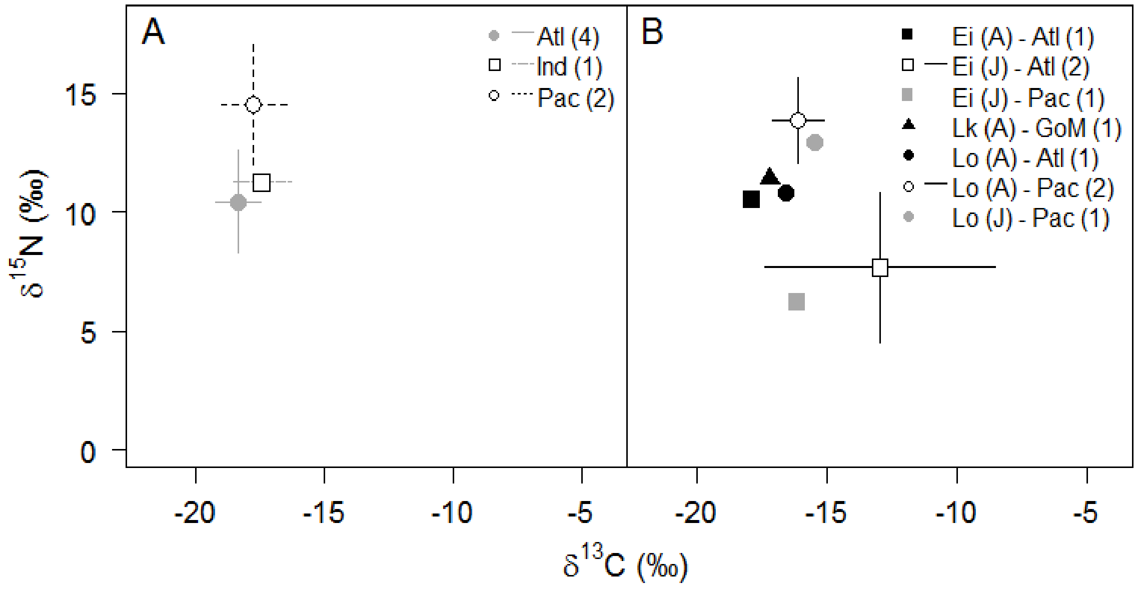

Fig. S2. Intraspecific variation of δ^{13}C and δ^{15}N values for (A) adult leatherback turtles and (B) Ei: hawksbill; Lk: Kemp's ridley; Lo: olive ridley turtles. Mean ±SD shown where n > 1. Number of studies contributing are shown in parentheses. A: adult; J: juvenile; Atl: Atlantic Ocean; GoM = Gulf of Mexico; Ind: Indian

CHAPTER 3: FORAGING ECOLOGY OF MEDITERRANEAN JUVENILE LOGGERHEAD TURTLES: INSIGHTS FROM C AND N STABLE ISOTOPE RATIOS

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Abstract

Bycatch is one of the key threats to juvenile marine turtles in the Mediterranean Sea. As fishing methods are regional or habitat specific, the susceptibility of marine turtles may differ according to inter- and intrapopulation variations in foraging ecology. An understanding of these variations is necessary to assess bycatch susceptibility and to implement region-specific management. To determine if foraging ecology differs with region, sex, and size of juvenile loggerhead turtles (*Caretta caretta*), stable isotope analysis of carbon and nitrogen was performed on 171 juveniles from a range of foraging regions across the central and eastern Mediterranean Sea. Isotope ratios differed with geographical region, likely due to baseline variations in $\delta^{13}C$ and $\delta^{15}N$ values. The absence of sex-specific differences suggests that within an area, all comparably-sized animals likely exploit similar foraging strategies, and therefore, their susceptibility to fisheries threats will likely be similar. The isotope ratios of juveniles occupying the North East Adriatic and North Levantine basin increased with size, potentially due to increased consumption of more prey items at higher trophic levels from a more neritic source. Isotope ratios of juveniles with access to both neritic and oceanic habitats did not differ with size which is consistent with them consuming prey items from both habitats interchangeably. With foraging habitats exploited differently among size classes in a population, the susceptibility to fisheries interactions will likely differ with size, therefore, region-specific management approaches will be needed.

Introduction

For globally distributed species, variation in life history and behavioural traits can improve resilience and survival in a changing environment (Jiguet et al. 2007; Bernhardt and Leslie 2013; Timpane-Padgham et al. 2017). Variability in the spatial and foraging ecology of a species may occur based on many factors, including morphological (e.g. size) or demographic (e.g. sex) parameters, or as a response to the environment, and can help reduce intraspecific competition (Werner and Gilliam 1984; Violle et al. 2012). For example, idividuals may consume different prey items resulting in individual specialisation in a generalist population (e.g. Vander Zanden et al. 2010; Thomson et al. 2018). As different individuals may play different roles within an ecosystem (Chapin et al. 2001; Violle et al. 2012) their susceptibility to disturbances, whether natural or anthropogenic, will also differ. Therefore, these variations in resource exploitation could influence population growth and dynamics (Araújo et al. 2011), complicating conservation management and requiring region specific management approaches.

Loggerhead turtles (*Caretta caretta*) demonstate complex life history patterns, utilising a wide range of ecosystems throughout their life cycle and facing various natural and anthropogenic threats at each life stage (Bolten 2003). Loggerhead turtle life history patterns and foraging strategies vary globally, and large gaps remain in our knowledge owing to the difficulty of monitoring such long lived animals at sea (Wildermann et al. 2018). Globally, fisheries bycatch is one of the most significant threats faced by marine turtles (Lewison et al. 2014). The extent of fishing and the fishing techniques used, drastically differs with location and habitat type (Casale 2011). Therefore, to better understand fisheries interactions and for successful conservation of loggerhead turtle populations, it is neccesary to understand inter- and intra-population variations in habitats used and resources exploited (Hamann et al. 2010; Rees et al. 2016).

To investigate the spatial and foraging ecology of juvenile loggerhead turtles, satellite telemetry deployed at foraging grounds has previously been used and can provide fine-scale near real-time movement data (e.g. McClellan and Read 2007; Mansfield et al. 2009; Arendt et al. 2012). However, satellite telemetry does not provide dietary information and the expense of this tool can often limit the sample size (Godley et al. 2008). Detailed information can be gained about the foraging ecology of individuals by analysing stomach contents and stable isotopes from stranded or incidentally captured individuals (Tomás et al. 2001; Revelles et al. 2007; Seney and Musick 2007; Casale et al. 2008; Lazar et al. 2011; Cardona et al. 2012, 2015; Blasi et al. 2018). Investigating stomach contents enables taxonomic identification of prey items but does bias against rapidly digested soft-bodied prey, represents a short dietary time frame (Duffy and Jackson 1986), and requires expertise, time, and access to freshly dead individuals. Stable isotope analysis (SIA) is a powerful cost-effective forensic tool that has been used to gain insights into the spatial and foraging ecology of numerous marine taxa (Rubenstein and Hobson 2004; Newsome et al. 2010; Bird et al. 2018), including marine turtles (Figgener et al. 2019a,b; Haywood et al. 2019). The ratio of stable isotopes within low-metabolically active tissues (e.g. epidermis and keratinised tissues such as scutes) reflects the food that an individual has consumed and the location where it was ingested (DeNiro and Epstein 1978). These tissues typically have slow turnover rates and the isotope incorporation from dietary items takes several months, and therefore represents diet over longer time frames than stomach content analysis (Reich et al. 2008).

The carbon isotope ratio (expressed as $\delta^{13}C$) of a consumer reflects the primary producer at the base of their food chain (DeNiro and Epstein 1978), with benthic and near-shore food chains supported by macroalgae and seagrass exhibiting high $\delta^{13}C$ values in comparison to pelagic and oceanic food chains supported by phytoplankton (DeNiro and Epstein 1978; Graham et al. 2010). The nitrogen isotope ratio (expressed as $\delta^{15}N$) at the base of a food chain differs in relation to (1) $\delta^{15}N$ values of their nutrient sources (e.g. N_2, ammonium, and nitrate), (2) nitrogen-based processes, including; nitrification, denitrification, and N_2-fixation, and (3) isotopic fractionation (Montoya 2007). On local-scales nitrogen isotope ratios, and to a lesser extent, carbon isotope ratios, can reflect trophic patterns within a food chain due to isotopic fractionation. With each subsequent trophic level, a 3-4‰ and a ~1‰ step wise increase in $\delta^{15}N$ and $\delta^{13}C$ values, respectively, are considered to occur (DeNiro and Epstein 1978; Minagawa and Wada 1984; France and Peters 1997).

As local-scale variations in stable isotope ratios can be inferred as differences in foraging grounds used or prey items consumed, they allow for the spatial and foraging ecology of loggerhead turtles to be assessed (e.g. Thomson et al. 2012; Ramirez et al. 2015; Turner Tomaszewicz et al. 2017). This is particularly useful for juvenile loggerhead turtles in the Mediterranean Sea, which have complex spatial and foraging ecology (see Casale et al. 2018 for a review of the biology of loggerhead turtles in the Mediterranean). Juveniles can be found throughout the Mediterranean in oceanic or neritic foraging grounds (Casale et al. 2018). Identifying foraging grounds is challenging and large data gaps remain in many areas of the Mediterranean, in particular the oceanic waters of the Levantine Basin (Casale et al. 2018). Fisheries bycatch data suggests major oceanic foraging grounds include the northern Ionian/South Adriatic, the southern Ionian/Sicilian Strait, and the westernmost part of the Mediterranean (Casale et al. 2011) and satellite telemetry highlighted the Tyrrhenian Sea, Algerian Sea, the Ionian as areas of importance (Zbinden et al. 2008; Hays et al. 2014a; Mingozzi et al. 2016; Luschi et al. 2018). Foraging in these oceanic regions is likely driven by the occurrence of patchy ephemeral resources due to eddies concentrating resources (Eckert et al. 2008). Neritic foraging grounds, were located in areas of high productivity and on the continental shelves of the Aegean Sea, Adriatic Sea, eastern Levantine basin, northern Africa, and off Tunisia (see Casale et al. (2018) and citations within).

Juvenile Mediterranean loggerhead turtles are considered highly opportunistic foragers with diverse dietary items reported across the Mediterranean (e.g. Tomás et al. 2001; Casale et al. 2008; Lazar et al. 2008). Stomach contents of strandings in North Cyprus were dominated by benthic prey items including bivalves and sponges (unpubl data). In comparison, the diet of juveniles caught in the Central Mediterranean were dominated by benthic prey items, including Malacostraca, Gastropoda, and Echinoidea, as well as pelagic prey items (Casale et al. 2008). In the western Mediterranean juveniles caught predominantly in neritic habitats had consumed both pelagic and benthic-demersal prey, including fish, pelagic tunicates, crustaceans, molluscs and other invertebrates (Tomás et al. 2001). Whilst in the Northern Adriatic, small juveniles that would have previously been considered oceanic in size had diets dominated by benthic items such as anemones, crustaceans, and molluscs (Lazar et al. 2008).

Mediterranean juveniles appear to follow alternative life history patterns to those in other ocean basins and intra-population differences in habitat use are also reported (Casale et al. 2008, 2015). In regions, such as Amvrakikos Gulf (Greece) and Cyprus, most individuals found in coastal neritic habitats are larger (mean CCL: 0.67 and 0.65 m, respectively; Rees et al. 2013; Snape et al. 2013). This supports the traditional ontogenetic life history model of a distinct shift in preference from oceanic to neritic habitat use with increased size (Musick & Limpus 1997). This traditional life history model is challenged on the Tunisian Plateau, Northern Adriatic Sea, and in the western Mediterranean, where juveniles as small as 0.25 m in length (notch-to-tip, Bolten 1999) start to utilise both neritic and oceanic habitats interchangeably, and are therefore, susceptible to threats in both habitats (Tomás et al. 2001; Casale et al. 2008; Lazar et al. 2008a, 2011).

In the Mediterranean Sea, bycatch is one of the key threats to marine turtles resulting in high levels of mortality in both neritic and oceanic habitats (conservatively 44,000 deaths per year, Casale 2011; Casale et al. 2018). The susceptibility of juvenile loggerhead turtles to anthropogenic threats differs with region due to heterogeneity in fishing effort as well as due to differences in habitat use by turtles (e.g. Cardona et al. 2009; Casale 2011). To loggerhead turtles foraging in neritic habitats the threat comes from small-scale fisheries using nets (trammel and gill) and bottom-set longlines whilst interactions with pelagic longline are more common for oceanic foragers (Casale 2011). Region and habitat use will also likely affect the susceptibility of marine turtles to other anthropogenic threats such as the ingestion of debris and chemical pollution (Franzellitti et al. 2004; Casale et al. 2008, 2016). Understanding the foraging habitats used by all individuals within and among populations is necessary in order to assess threats and implement appropriate management approaches. Therefore, using SIA of stranded, incidentally and directly captured juveniles, this study aims to assess the foraging ecology of juvenile loggerhead turtles from a range of foraging regions in the Mediterranean Sea, to determine if foraging ecology differs with region, sex, and size.

Materials and methods

2.1 Sample collection

Carapace costal scute samples were obtained from dead incidentally captured juvenile loggerhead turtles found in the NE Adriatic (Croatia and Slovenia, n=52) and Central Mediterranean (Lampedusa, n=36, Fig 1) between

2001 and 2006. These turtles were captured by trawl, longline, or static net fishing gear. Scute samples were taken by scalpel from the second or third costal scute. The exact location of the incidentally captured individuals in the Central Mediterranean is unknown as turtles were collected from fishers on the Tunisian continental shelf and landed in Lampedusa. In the North Levantine basin (North Cyprus), 228 juveniles were stranded dead or incidentally captured (dead and alive in trammel nets) between 2012 and 2018. Of these, 65 were sampled for epidermis tissue (<0.25 cm^2, Fig 1) from the trailing edge of the fore flipper on the third membrane or the shoulder (between the neck and fore flipper). Epidermis tissue samples were also collected from the third membrane from the trailing edge of the fore flipper of live-captured juveniles foraging in the East Ionian (Amvrakikos Gulf, Greece, n=18, Fig 1) in 2017 (see Rees et al. 2013 for details on the capture method). Skin samples were taken by scalpel and only the epidermis tissue was used in the analysis (dermis tissue was removed in the laboratory). Until required for analysis, scute samples were air-dried then frozen and epidermis samples were stored in ethanol (90% and 70% ethanol in East Ionian and North Levantine basin, respectively) at room temperature.

Curved carapace length (CCL) was measured with a flexible measuring tape as an indicator of body size. CCL measurements in the Central Mediterranean, East Ionian, and NE Adriatic were notch-to-tip, whilst CCL measurements in the North Levantine basin were notch-to-notch (Bolten 1999; for conversion of notch-to-tip to notch-to-notch values see Appendix S1). Individuals were considered juvenile if CCL<0.80 m, which is the rookery-weighted mean size at sexual maturity for Mediterranean loggerhead turtles, and was selected as genetics suggest mixed stocks in the foraging grounds (Casale et al. 2005, 2018; Casale and Heppell 2016). For dead juveniles, sex was determined by gross morphology and/or histology of the gonads (Casale et al. 2006; Lazar et al. 2008b), whilst sex was unknown for live-caught and live-bycaught juveniles in the East Ionian and North Levantine basin, respectively, as sex is not usually dimorphic at juvenile stages and gross morphology of the gonads could not be performed.

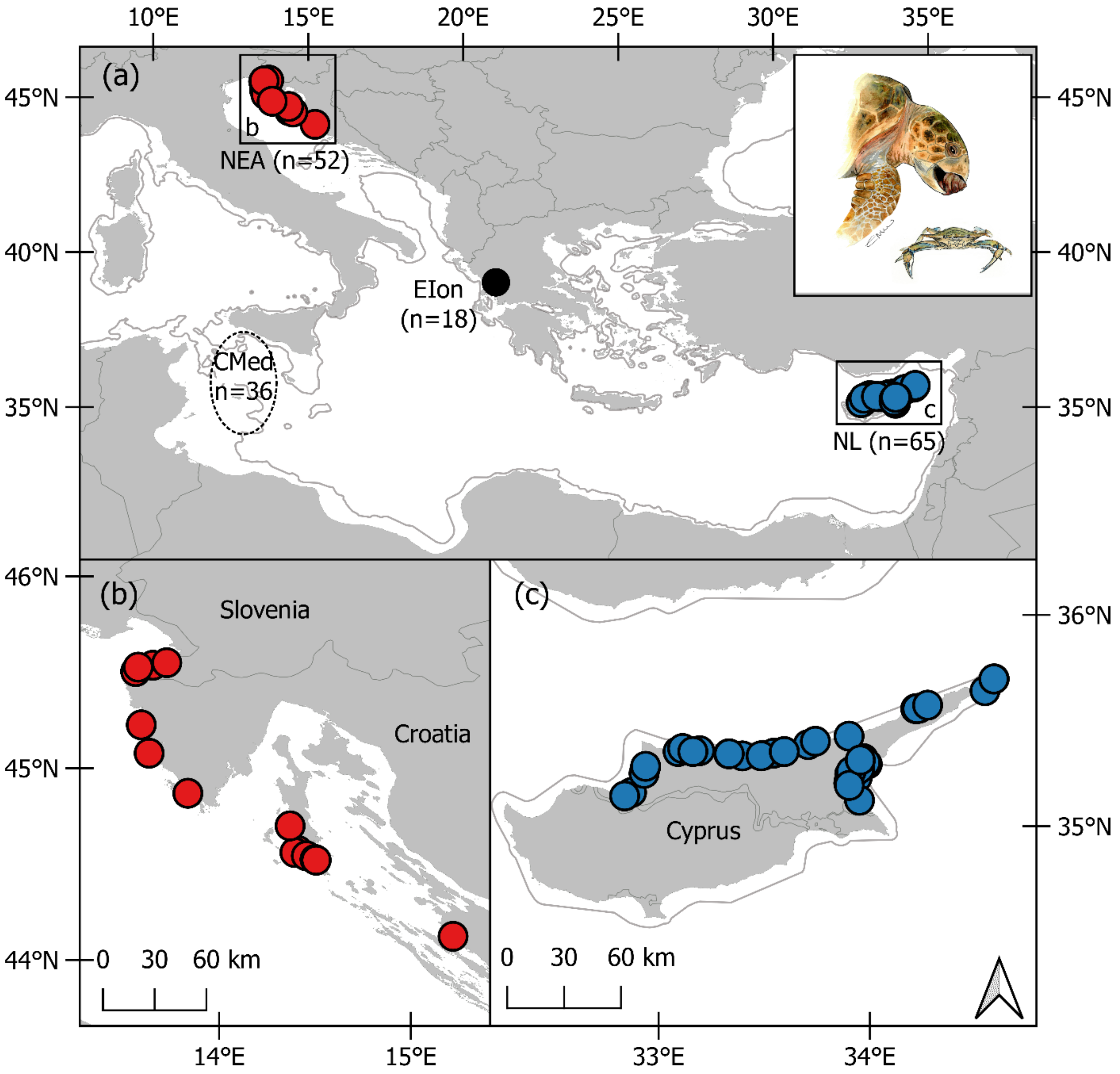

Fig. 1 (a) Locations of juvenile loggerhead turtles sampled in the Central Mediterranean (CMed, open circle – at sea locations are unknown), East Ionian (EIon, black circle), NE Adriatic (NEA, red circles), and North Levantine basin (NL, blue circles). The location where juveniles were sampled is shown in (b) for the NE Adriatic and (c) for the North Levantine basin. 200 m isobath is indicated (grey line). Artwork inset of a loggerhead turtle foraging

2.2 Stable isotope analysis

Scute samples were cleaned to remove epibionts and rinsed with ethanol. Both scute and epidermis samples were rinsed with deionized water, soaked for 24 hours, and dried at 60 ˚C for 48 hours. Approximately 0.70 mg (±0.10 mg) of sample was weighed in to sterilised tin capsules. Epidermis samples did not undergo lipid extraction and did not require a lipid correction factor as evaluated by the C:N ratio (mean:3.44, range: 3.18-3.78, Post et al. 2007). Samples were analysed on a Thermoquest EA1110 elemental analyser linked to a Sercon2020 stable isotope ratio mass spectrometer running in continuous flow mode (conducted by Elemtex Ltd, UK laboratory). Isotope ratios are expressed as conventional delta (δ) values in parts per thousand (‰) using the following equation: $\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$, where X is ^{13}C or ^{15}N. R_{sample} and $R_{standard}$ are the corresponding ratios of the heavier to the lighter isotope (i.e. $^{13}C/^{12}C$, $^{15}N/^{14}N$) in the sample and international standard, respectively. The international standard, for ^{13}C and ^{15}N is Vienna Pee Dee Belemnite and atmospheric nitrogen (AIR), respectively.

All analyses were performed with the software R 3.5.1 (R Core Team 2018) and for statistical tests, the significance level used was $\alpha = 0.05$. To determine if region affects $\delta^{13}C$ and $\delta^{15}N$ values, whilst taking size into account, an Analysis of Covariance was performed. To determine if sex affected stable isotope ratios an Analysis of Variance (ANOVA) was performed whilst a General Additive Model (GAM) was performed using the R package 'mgcv' (Wood 2011) to determine if size affected $\delta^{13}C$ and $\delta^{15}N$ values, with size set as a smooth term.

The isotopic niche width of individuals grouped by region or sex was calculated using the R package 'SIBER' (Stable Isotope Bayesian Ellipses in R, Jackson et al. 2011). Maximum likelihood standard ellipses were obtained by Bayesian inference containing 40% of the data (SEA) and small samples sizes were corrected for (SEA_c). Isotope niche overlap among each group was calculated as the proportion of the non-overlapping area of the two ellipses. See Jackson et al. (2011) for details on these methods.

The time between death and sampling is unknown for stranded individuals, however, decomposition is not thought to affect $\delta^{13}C$ and $\delta^{15}N$ values of loggerhead turtle epidermis (Payo-Payo et al. 2013). We compared the stable isotope ratios of juveniles with different decomposition states (categorised as: alive, fresh dead, moderately decomposed, severely decomposed, and skeleton) and found no significant differences and therefore for further analysis individuals were not analysed seperately based on decomposition state. Stable isotope ratios of stranded and incidentally captured juveniles from the North Levantine basin did not differ isotopically and therefore from herein were treated as one group and referred to as stranded unless specified otherwise (for details on these analyses see Appendix S2). To determine temporal shifts in baseline ratios for each region, stable isotope ratios were compared across the sampling periods using ANOVAs. To determine monthly differences in the δ^{13}C and δ^{15}N values of epidermis samples from the North Levantine basin, Generalised Additive Mixed Models (GAMM) were used in the R-package ‘mgcv’ (Wood, 2011). The GAMM used a cyclic smoothing spline to account for the annual cyclic trend.

Results

In total, tissue from 171 juveniles were analysed from the Central Mediterranean, East Ionian, NE Adriatic, and North Levantine basin (Table 1). δ^{13}C values ranged from -19.32 to -12.76‰ (mean ± SD = -16.60 ± 1.34‰, n=171) and δ^{15}N values ranged from 3.94 to 13.71‰ (mean ± SD = 8.03 ± 2.14‰, n=171). For 18 individuals, replicate scute samples were analysed but, no significant difference was found between replicates for δ^{13}C and δ^{15}N values (Wilcoxon signed-ranks test, δ^{13}C: V=1657, Z=-1.10, *P*=0.27, n=88; δ^{15}N: V=1547, Z=-1.40, *P*=0.16, n=18) and as a result the mean value was used for further analysis. The results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5).

Table 1 Information on juvenile loggerhead turtles sampled in the Mediterranean. CCL: curved carapace length in meters, F: female, M: male, U: unknown.

Origin	Central Mediterranean	East Ionian	NE Adriatic	North Levantine basin
Tissue type	Carapace	Epidermis	Carapace	Epidermis
Sample size	36	18	52	65
Sex	F:16, M:20, U:0	F:0, M:0, U:18	F:33, M:12, U:7	F:21, M:16, U:28
CCL mean ± SD (range)	0.43 ± 0.11 (0.24 to 0.74)	0.68 ± 0.05 (0.61 to 0.75)	0.45 ± 0.14 (0.23 to 0.78)	0.63 ± 0.11 (0.12 to 0.77)
δ^{13}C mean ± SD (range, ‰)	-18.25 ± 1.34 (-19.32 to -14.71)	-15.16 ± 0.49 (-15.90 to -14.00)	-16.94 ± 0.77 (-18.99 to -15.20)	-15.83 ± 0.99 (-17.60 to -12.76)
δ^{15}N mean ± SD (range, ‰)	6.17 ± 2.14 (3.94 to 9.71)	8.43 ± 1.15 (7.10 to 10.80)	10.16 ± 1.52 (6.19 to 12.55)	7.25 ± 1.64 (4.80 to 13.71)
Sampling period	2001 - 2003	2017	2003 - 2006	2012 - 2018

To determine temporal shifts in baseline ratios for each region, stable isotope ratios were compared across the sampling periods. Neither δ^{13}C nor δ^{15}N values differed with year in all regions (ANOVA, Central Mediterranean: δ^{13}C: $F_{(2,19)}$=0.15, *P*=0.86, δ^{15}N: $F_{(2,19)}$=0.90, *P*=0.42, n=36; NE Adriatic: δ^{13}C: $F_{(4,46)}$= 0.13, *P*=0.97, δ^{15}N: $F_{(4,46)}$=0.10, *P*=0.98, n=52; North Levantine basin: δ^{13}C: $F_{(6,58)}$= 1.28, *P*=0.28, δ^{15}N: $F_{(6,58)}$=2.13, *P*=0.06, n=65, see Appendix S3). These results were found to be insensitive to the isotope analytical uncertainties, however, note the higher uncertainties (resulting in a lower performance consistency for nitrogen) for the North Levantine basin (for details of this analysis see Appendix S5). East Ionian samples were not included in this analysis as all samples were collected in 2017 only. A significant difference was seen in $\delta^{13}C$ values with month for the samples collected in the North Levantine basin (GAMM: F=1.53, edf=2.32, p<0.002, R^2=0.17, n=4) with higher $\delta^{13}C$ values in the summer months (Fig S4.4). No difference was seen in $\delta^{15}N$ values with month (GAMM: F=1.53, edf=2.32, p<0.002, R^2=0.17, n=4, Fig S4.4). These results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5).

3.1 Inter-region differences

A significant difference was seen in $\delta^{13}C$ values among regions (ANOVA, $F_{(3,167)}$= 80.49, *P*<0.001, n=171) and a post hoc Tukey's Honest Significant Difference test showed this was due to the $\delta^{13}C$ values of all regions differing with juveniles from Central Mediterranean having the lowest values (*P*<0.001, Fig 2). When body size was taken into account, region continued to affect $\delta^{13}C$ values (ANCOVA, $F_{(3,163)}$= 81.80, *P*<0.001, n=171). A significant difference was seen in $\delta^{15}N$ values among regions (ANOVA: $F_{(3,167)}$= 59.99, *P*<0.001, n=171) and a post hoc Tukey's Honest Significant Difference test shows this was due to the $\delta^{15}N$ values of all regions differing with juveniles from NE Adriatic having the highest values (*P*<0.001, Fig 2). When body size was taken into account, region continued to affect $\delta^{15}N$ values (ANCOVA, $F_{(3,163)}$= 63.78, *P*<0.001, n=171). These results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5). SIBER results show the isotope niche of Central Mediterranean and NE Adriatic juveniles are distinct as their overlaps were null, whilst juveniles in the North Levantine basin slightly overlapped with East Ionian juveniles (Table 2, Fig 2).

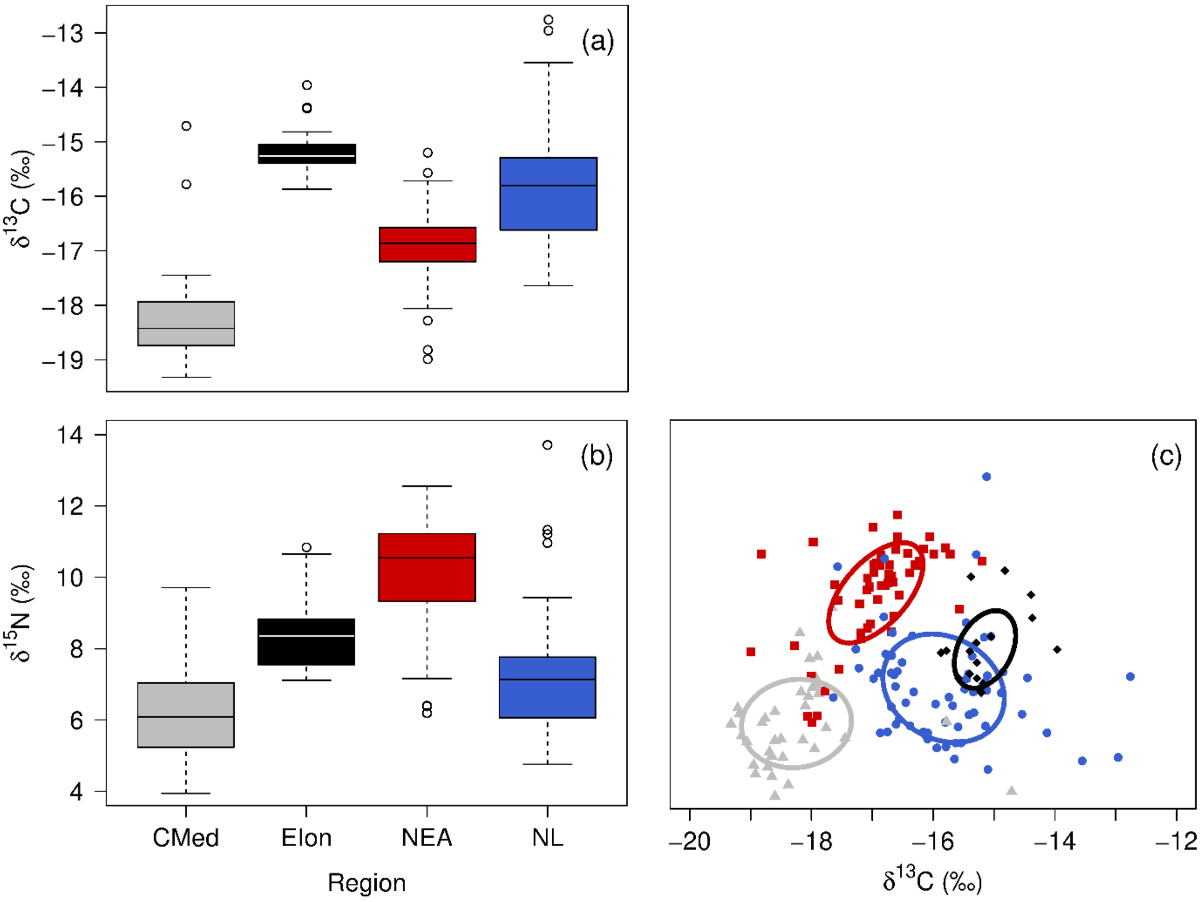

Fig. 2 (a) δ^{13}C values and (b) δ^{15}N values of juvenile loggerhead turtles sampled in the Central Mediterranean (CMed, grey, n=36), East Ionian (EIon, black, n=18), NE Adriatic (NEA, red, n=52), and the North Levantine basin (NL, blue, n=65). Midline = median, box = interquartile range, whiskers = 5 and 95 percentiles. (c) Bivariate plot of δ^{13}C and δ^{15}N values showing the isotope niche coloured by region. Ellipses = Standard ellipse area corrected for small sample size (SEA$_c$) created by SIBER

3.2 Sex-specific differences

In total, sex was determined for 36 juveniles in the Central Mediterranean (F=16, M=20), 45 in the NE Adriatic (F=33, M=12), and 37 in the North Levantine basin (F=21, M=16). Neither δ^{13}C nor δ^{15}N values differed between female and male juvenile loggerhead turtles within each region (ANOVA, Central Mediterranean: δ^{13}C: $F_{(1,34)}$ =0.87, *P*=0.36, δ^{15}N: $F_{(1,34)}$ =1.92, *P*=0.17, n=36; NE Adriatic: δ^{13}C: $F_{(1,43)}$ =3.15, *P*=0.08, δ^{15}N: $F_{(1,43)}$ =0.10, *P*=0.76, n=45; North Levantine basin: δ^{13}C: $F_{(1,35)}$ =0.02, *P*=0.90, δ^{15}N: $F_{(1,35)}$ =1.72, *P*=0.20, n=37, Fig 3). These results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5). SIBER results show the isotope niche of females and males are not distinct in any region (Table 2, Fig 3).

Table 2 Summary results of SIBER. CMed: Central Mediterranean, EIon: East Ionian, NEA: NE Adriatic, NL: North Levantine basin, SEA: Standard ellipse area, SEA_c: Standard ellipse area corrected for small sample size, Overlap: isotope niche overlap among each group calculated as the proportion of the non-overlapping area of the two ellipses

			Region			
			CMed	EIon	NEA	NL
Region	SEA		3.72	1.65	3.01	5.02
	SEA_c		3.83	1.75	3.07	5.10
	Overlap	CMed		<0.001	<0.001	<0.001
		EIon			<0.001	0.11
		NEA		-	-	<0.001
Sex	SEA	Female	3.97	NA	2.17	5.18
		Male	3.20	NA	2.99	2.59
	SEA_c	Female	4.25	NA	2.24	5.45
		Male	3.38	NA	3.28	2.77
	Overlap		0.42	NA	0.43	0.50

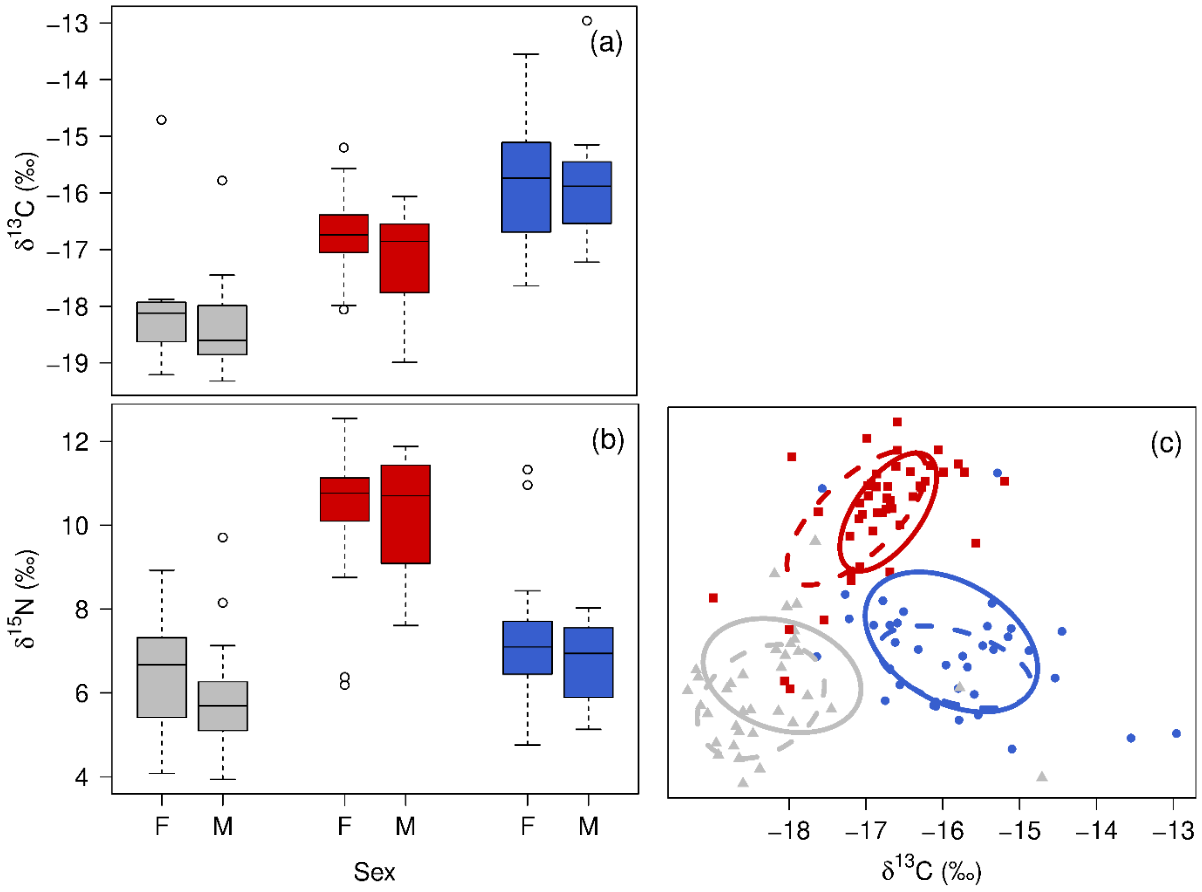

Fig. 3 (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values of female and male juvenile loggerhead turtles sampled in the Central Mediterranean (grey, n: F=16, M=20), NE Adriatic (red, n: F=33, M=12), and North Levantine basin (blue, n: F=21, M=16). F: Female, M: male. Midline = median, box = interquartile range, whiskers = 5 and 95 percentiles. (c) Bivariate plot of $\delta^{13}C$ and $\delta^{15}N$ values showing the isotope niche of females (solid lines) and males (dashed lines) coloured by region. Ellipses = Standard ellipse area corrected for small sample size (SEA_c) created by SIBER. Sex was unknown for East Ionian juveniles as they were live-caught

3.3 Size differences

A full range of juvenile sizes were sampled from 0.12 to 0.79 m (mean CCL = 0.54 m). Size significantly differed among regions (ANOVA, $F_{(3,167)=}40.8$, $P<0.001$, n=171). A post hoc Tukey’s Honest Significant Difference test showed juveniles sampled from the East Ionian and the North Levantine basin were significantly larger than juveniles from the Central Mediterranean and NE Adriatic ($P<0.001$). The $\delta^{13}C$ values of juvenile loggerhead turtles were not affected by size in any region (GAM, $P>0.05$, Fig 4). The $\delta^{15}N$ values were not affected by size in the Central Mediterranean or East Ionian whilst larger individuals had higher $\delta^{15}N$ values in the NE Adriatic (GAM, F=7.24, $P=0.009$) and the North Levantine basin (F=3.05, $P=0.04$, Fig 4). These results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5).

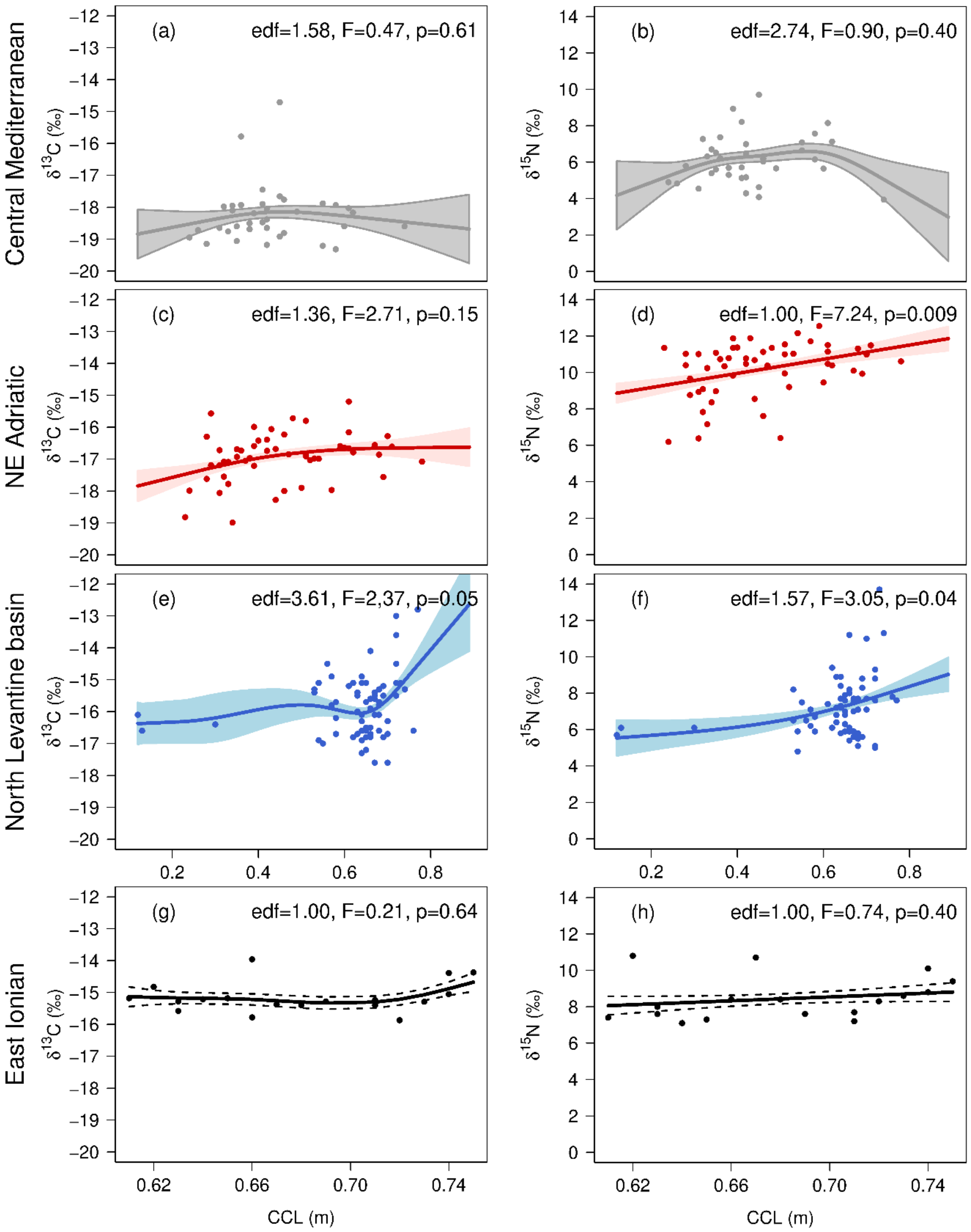

Fig. 4 Summary of the influence of curved carapace length (CCL) on δ^{13}C values (left column) and δ^{15}N values (right column) of juvenile loggerhead turtles sampled in the (a,b) Central Mediterranean, (c,d) NE Adriatic, (e,f) North Levantine basin, and (g,h) East Ionian. Solid line represents mean isotope ratio response and shaded region represents ± standard error. Edf: estimated degrees of freedom, F: F-statistic, p: significance. Note different x-axis for East Ionian plots

Discussion

The results highlight the ecological complexity of Mediterranean juvenile loggerhead turtles and demonstrates the benefits of conducting SIA on opportunistically obtained juveniles for understanding the foraging ecology of marine vertebrates. Regional differences are observed in stable isotope ratios, and intra-regional variation occurs with size but not sex, therefore supporting a requirement for site specific management approaches.

4.1 Inter-region differences

Differences in stable isotope ratios among regions are more likely due to baseline variations in $\delta^{13}C$ and $\delta^{15}N$ values rather than geographical differences in foraging ecology. The Central Mediterranean sampling region is offshore (~160 km), surrounded by both neritic and oceanic habitats, from which loggerhead turtles forage (Casale et al. 2008). Although on the continental shelf, food chains in this offshore region are likely supported by phytoplankton, which have lower $\delta^{13}C$ values in comparison to productive benthic and nearshore regions with food chains supported by algae and seagrass (DeNiro & Epstein, 1978; Graham et al. 2010). This likely explains why juveniles foraging in the Central Mediterranean have lower $\delta^{13}C$ values than juveniles foraging in the East Ionian, NE Adriatic, and North Levantine basin, which are likely foraging predominantly in neritic habitats. This trend has been observed in several loggerhead turtle populations (e.g. Hatase et al. 2002; Eder et al. 2012). Although a stepwise enrichment in $\delta^{13}C$ values can be seen with each subsequent trophic level it is unlikely juveniles foraging in the Central Mediterranean are foraging at lower trophic levels than the other regions as they do not have lower $\delta^{15}N$ values (except in comparison to the NE Adriatic, DeNiro and Epstein 1978; Minagawa and Wada 1984; France and Peters 1997).

High $\delta^{15}N$ values have been previously reported for loggerhead turtles foraging in the NE Adriatic and has been attributed to the extensive influence of highly enriched ^{15}N agricultural run-off and anthropogenic waste from major river systems (Degobbis and Gilmartin 1990; Zbinden et al. 2011; Cardona et al. 2014; Haywood et al. 2020). In comparison, relatively low baseline $\delta^{15}N$ values are seen across the eastern Mediterranean basin, which includes the North Levantine basin and the Central Mediterranean and is most likely due to high levels of N_2-fixation (Pantoja et al. 2002).

Differences in sampling methods among the geographical regions may also bias the results. For example, the sampling area of each geographical region differs substantially with the East Ionian individuals sampled from a discrete neritic site in the Amvrakikos Gulf with limited foraging options (max depth 65m, Rees et al. 2013), the NEA Adriatic and North Levantine basin were sampled in a relatively discrete area, whereas a large area was fished in the Central Mediterranean where juveniles likely had access to multiple foraging habitats (Casale et al. 2008). Sampling method differed with region with individuals in the East Ionian live caught in targeted foraging grounds, individuals from Central Mediterranean and NE Adriatic incidentally captured, whilst individuals from the North Levantine basin were incidentally captured or stranded. The cause of stranding was often unidentified and the location in which the turtle died was unknown.

In addition, incidentally captured individuals were caught in different fishing gears dependent on the geographical region. In the North Levantine basin individuals were incidentally captured in trammel nets therefore incidentally targeting neritic foragers, whilst individuals caught in the Central Mediterranean and NEA Adriatic were caught by trawl, longline, or static net fishing gear, and in turn sampling either benthic or pelagic habitats. The SIBER results, show that juveniles in the East Ionian have the narrowest isotopic niche, which may be due to limited foraging options or due to the small sample size (although small sample sizes were corrected for). Juveniles in the Central Mediterranean and NE Adriatic have relatively small isotope niche widths, whilst juveniles foraging in the North Levantine basin had the largest. The larger isotope niche width seen for North Levantine basin juveniles could suggest they are foraging on a larger range of prey or are using a larger range of habitats. The mean size (CCL) at sexual maturity for loggerhead turtles in the Mediterranean is considered 0.80 m (Casale and Heppell 2016), but, females nesting in North Cyprus and foraging in other regions of the Mediterranean can be considerably smaller (minimum recorded was 0.59 m, unpublished data). Therefore, some of the individuals sampled in the North Levantine basin and assigned as juveniles may in fact nest in North Cyprus but forage in other areas of the Mediterranean, resulting in a large isotope niche width for the North Levantine basin group.

It should be noted that in this study two tissues types, scute and epidermis, were used. The isotope ratios represent a time intergrated diet with each tissue type respresenting different time frames of dietary information due to differences in the metabolic turnover rate (Peterson & Fry 1987). Epidermis incorporates dietary information over several months (Reich et al. 2008), whilst scute represents a longer time frame (e.g. Vander Zanden et al. 2010). This is not an issue when studying adults as they are known to show high foraging site fidelity and therefore have relatively constant isotope ratios through their scutes. However, this can be a limitation for juvenile loggerhead turtles in the Mediterranean as although some remain in distinct grounds others have been found to shift habitats relativley frequently (e.g. Cardona et al. 2005, 2009; Casale et al. 2007, 2012; Eckert et al. 2008). Epidermis samples from the North Levantine basin show a seasonal change in carbon isotope ratios demonstrating a potential habitat or dietary shift through the year and may explain the larger isotope niche reported in this region. Scute samples analysed from Central Mediterranean and NE Adriatic juveniles may therefore represent a combination of several habitats and prey items. As juveniles from these regions had distinct isotope ratios, relatively small isotope niche widths, and isotope ratios that match the current knowledge about the isoscape of the Mediterranean, it suggests that even if these individuals are frequenting several habitats they are likely remaining in the same geographical region.

Although tissue-tissue conversion equations enable isotopes ratios from different tissue types to be compared, they should be used with caution as there are numerous factors that can influence isotopic differentiation between tissues. Therefore, we support previous reccomendations that a standardised tissue type should be used enabling direct comparisons between studies especially when investigating juveniles (see Haywood et al. 2019 and citations within).

4.2 Sex-specific differences

Differences between resource use of female and male adults might be expected due to various evolutionary and energetic pressures related to reproduction (Pajuelo et al. 2016), although differences may not be evident until they have reached sexual maturity. No difference in the foraging ecology of female and male loggerhead turtles has been documented previously in the

Mediterranean or other ocean basins (Tomás et al. 2001; Seney and Musick 2007; Schofield et al. 2010, 2013; Pajuelo et al. 2012; Thomson et al. 2012; Casale et al. 2013; Hays et al. 2014b). The absence of sex-specific differences in stable isotope ratios, the high overlap in isotope niche, and the similar sex ratios at each sample site, suggests juvenile males and females exploit similar prey items and inhabit similar areas. With both sexes utilising the same resources, their susceptibility to fisheries threats will likely be similar. This supports the findings of an unbiased sex ratio of bycaught juveniles in the Mediterranean Sea previously reported by Casale et al. (2006).

4.3 Size differences

Higher $\delta^{13}C$ and $\delta^{15}N$ values with size have been previously reported for both juvenile and adult loggerhead turtles in the Mediterranean and other ocean basins (Godley et al. 1998; Hatase et al. 2002; Pajuelo et al. 2010; Eder et al. 2012; Goodman Hall et al. 2015; Ramirez et al. 2015; Blasi et al. 2018), but this is not always the case (Wallace et al. 2009; Clusa et al. 2016). This suggests shifts in habitat use or diet with size are not obligate, and a relaxed life history model has been previously reported in the Mediterranean Sea (Casale et al. 2008). Higher $\delta^{15}N$ values in larger juveniles could suggest larger individuals are foraging in more neritic habitats which have comparatively higher baseline $\delta^{13}C$ and $\delta^{15}N$ values compared to oceanic habitats (Hatase et al. 2002; McClellan et al. 2010; Ramirez et al. 2015). This isotope ratio and size trend is well reported for populations undertaking oceanic-neritic ontogenetic shifts during the juvenile life stage (Snover et al. 2010; Ramirez et al. 2015; Turner Tomaszewicz et al. 2017).

However, it is very likely the loggerhead foraging grounds in the NE Adriatic and North Levantine basin are on the continental shelf and therefore differences in oceanic and neritic foraging habitat is less likely than differences in epi-pelagic verses benthic prey consumption. Due to trophic fractionation, higher trophic prey items have higher $\delta^{15}N$ values (DeNiro and Epstein 1978; Minagawa and Wada 1984; France and Peters 1997; Belicka et al. 2012). Improvement in diving capacity (depth and duration) as well as larger heads, larger gape size, and therefore higher bite force with size (Salmon et al. 2004; Marshall et al. 2012) means previously inaccessible higher trophic fauna, such as large molluscs, crustaceans, and fish, become available to larger individuals (Seney and Musick 2007, Casale et al. 2008; Goodman Hall et al. 2015; Blasi et al. 2018). This would explain the size trend observed in this study for juveniles foraging in the North Levantine basin and NE Adriatic, whilst the small size range in East Ionian turtles may explain why no size effects were reported. With trammel and gill nets, as well as bottom-set longlines, being the highest cause of bycatch in neritic habitats (Casale 2011), juvenile loggerheads may become more susceptible to neritic fishing gears in these regions as they grow, as they may be foraging on more neritic prey items.

In contrast, in the Central Mediterranean, Casale et al. (2008) reported benthic and epi-pelagic prey was commonly consumed in both neritic and oceanic individuals of all size classes. This not only suggests foraging throughout the water column, but the use of both neritic and oceanic habitats interchangeably (Casale et al. 2008). This was also found in the western Mediterranean with no differences in isotope ratios reported for juveniles caught in neritic or oceanic habitats or between individuals of different sizes suggesting the consumption of similar dietary items (Revelles et al. 2007). Hence, isotope ratios of an individual could incorporate baseline isotope ratios of both neritic and oceanic habitats and would explain why no size trend was seen in juveniles sampled from the Central Mediterranean in this study or for juveniles sampled in southern Italy by Clusa et al. (2016). With bycatch in the Central Mediterranean spanning both the neritic and oceanic habitats (as emphasised by samples in this region collected from trawl, pelagic longline, and static net fishing gear), the results from this study suggests juveniles in the Central Mediterranean maybe bycaught in both habitats throughout their size range.

4.4 Implications for conservation

SIA has been used globally to demonstrate size related differences in habitat use for loggerhead turtles and in turn highlighting the need for conservation management to consider population sub-groups (e.g. Hatase et al. 2002; McClellan et al. 2010; Snover e tal. 2010; Thomson et al. 2012; Ramirez et al. 2015; Turner Tomaszewicz et al. 2017). In neritic habitats, such as in the North Levantine basin, bottom-set fishing gear is most common (Casale 2011). With larger individuals potentially consuming a more benthic dominated diet this may increase the probability of bycatch in this size class. This has been previously reported by Snape et al. (2013) who found mostly larger individuals were bycaught in Cyprus and attributed most strandings to small-scale fisheries using demersal gears, which could cause a shift in population dynamics. In the water of eastern mainland Spain, juveniles appear to extensively use the continental shelf where their susceptibility to neritic fishing gears is high (Cardona et al. 2009). In comparison, with juveniles of all sizes utilising both neritic and oceanic habitats in the Central Mediterranean, interactions with both bottom-set gears and pelagic longlines are likely. This is supported by research by Clusa et al. (2016) that showed isotope and genetic markers of Atlantic and Mediterranean juveniles in the western and central Mediterranean differed with region but not between pelagic or neritic fishing gears. This suggests that these juveniles are using both habitats interchangeably and it was concluded that in these areas of the Mediterranean the impact of turtle bycatch depends on the geographic distribution of the fishing effort rather than the fishing type (Clusa et al. 2016) unlike in the North Levantine basin. With different foraging strategies used in different regions of the Mediterranean, region-specific management approaches are required, dependent on whether management of fishing gear or fishing location would be most beneficial.

Surface currents in the global oceans are thought to passively disperse loggerhead turtle hatchlings to the foraging grounds that they continue to return to throughout their life time (Hays et al. 2010; Putman et al. 2012; Scott et al. 2012; Casale & Mariani, 2014). The distinct isotope niche of juveniles in each geographical region in this study suggests a limited exchange of individuals between these areas and therefore supports the hypothesis that large juveniles remain in the same geographical region they passively drifted to.

With juveniles likely remaining in the same geographical region, the susceptibility to fisheries interactions will differ as fishing effort and fishing gear is not spatially homogenous across the Mediterranean (Casale 2011 and citations within). Marine turtles face other anthropological threats and the level of these also differs with region and habitat use (see review by Casale et al. (2018)). For example, in the north Adriatic, loggerhead turtles have high levels of heavy metals (Franzellitti et al. 2004), whilst low levels were reported in Cyprus turtles twenty years ago (Godley et al. 1999). Individuals with a higher trophic position are thought to have heavier burdens of pollutants due to diet related bioaccumulation

(Mckenzie et al. 1999). In addition, Central Mediterranean loggerhead turtles caught in pelagic habitats have higher rates of debris ingestion compared to those in neritic habitats (Casale et al. 2016). Therefore, for conservation management to be successful the spatial and foraging ecology of marine turtles must be considered.

To further enhance our understanding of the complexities of loggerhead turtle foraging ecology globally, we support the recommendations to (1) use additional forensic markers or complementary techniques to provide greater power of inference of dietary estimations and geographical differences, (2) for standardised methods to be used to allow comparisons across studies, and (3) for the collaboration and combining of datasets at a global scale (as reviewed in Haywood et al. (2019) and citations within).

Conclusions

This study highlights the use of stable isotope analysis to better understand the foraging ecology of marine vertebrates. For juvenile loggerhead turtles in the Mediterranean Sea, differences in foraging ecology do not occur between sexes but do occur among geographical regions and with size. Differences in stable isotope ratios among geographical regions are likely due to the different habitats used by each population, with individuals in the Central Mediterranean using more oceanic habitats than the other populations. Susceptibility of these regions to different fisheries will therefore be likely and should be considered in future management strategies. Size differences were region dependent with no differences reported in regions where oceanic and neritic habitats were available suggesting juveniles in these regions will be bycaught by multiple fishing gears throughout their size range. In regions with only neritic habitats, differences were attributed to larger individuals exploiting different prey, and suggests that individuals of different sizes may play different roles in the ecosystem and in turn become more susceptible to neritic fishing gears as they grow. These results confirm the necessity of implementing region as well as habitat specific management approaches.

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Data availability Statement The datasets collected and analysed during the current study are available from the corresponding author on reasonable request.

Conflict of Interest The authors have no conflicting interests.

Ethical approval All live turtles are either released immediately after sampling or placed under the care of a veterinary surgeon at a rehab centre.

Author contributions Annette Broderick, Brendan Godley, Jamie Shutler, Steve Widdicombe, and Wayne Fuller conceived the project ideas; Annette Broderick, ALan Rees, Brendan Godley, Bojan Lazar, Daniela Freggi, Dimitris Margaritoulis, Julia Haywood, Nathalie Swain-Diaz, Paolo Casale, Robin Snape, and Wayne

Fuller collected the data; Julia Haywood analysed the data and drafted the manuscript; Annette Broderick, Brendan Godley, and Jamie Shutler guided the writing with contributions from all authors. All authors read and approved the final manuscript.

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Supporting Information

Appendix S1 – Curved carapace length notch-to-tip and notch-to-notch conversion

To determine if notch-to-tip (N-T) and notch-to-notch (N-N) curved carapace lengths (CCL) can be used interchangeably, 26 loggerhead turtles stranded dead or bycaught (dead and alive) in the North Levantine basin (North Cyrpus) were measured for both variables. N-T and N-N did differ significantly (Paired t test, t=-12.72, df=25, p<0.001, n=26) with N-T being larger (mean ± SD = 0.66 ± 0.61 m) than N-N (mean ± SD = 0.65 ± 0.60 m). There was a strong positive correlation between N-T and N-N (Pearson's correlation, ρ=0.99, p<0.001, n=26, Fig S1.1), hence, N-T could be converted to N-N for further analysis using the conversion equations derived here from linear regressions ($F_{1,24}$=6902, p<0.001, $R^2_{(Adj)}$=0.99, Fig S1.1).

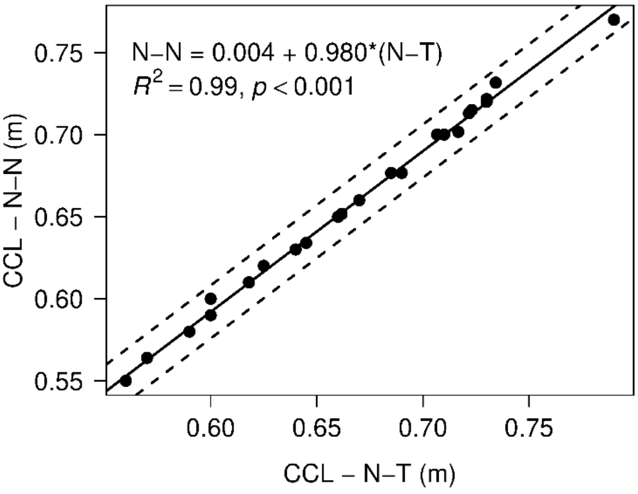

Fig. S1.1 Linear relationship between curved carapace lengths (CCL) notch-to-tip (N-T) and notch-to-notch (N-N) of loggerhead turtles sampled in the North Levantine basin (North Cyprus). Solid line depicts linear regression and dotted lines depict 95% confidence intervals. The conversion equation and regression statistics are shown

Appendix S2 – Isotopic differences with decomposition state and catch method

Individuals stranded in the North Levantine basin were either alive (n=18), fresh dead (n=18), moderately decomposed (n=10), severly decomposed (n=1), skeleton (n=1), or the decomposition state was unknown (n=19). Neither $\delta^{13}C$ nor $\delta^{15}N$ values differed with decomposition state (ANOVA, $\delta^{13}C$: $F_{(4,42)}=0.34$, p=0.85, $\delta^{15}N$: $F_{(4,42)}=1.48$, p=0.23, n=47, Fig S2.2) and therefore samples were considered one group for further analysis. Individuals found in the North Levantine basin were either bycaught (n=28) or stranded (n=27). Neither $\delta^{13}C$ nor $\delta^{15}N$ values differed with catch method (ANOVA, $\delta^{13}C$: $F_{(1,53)}=0.13$, p=0.72, $\delta^{15}N$: $F_{(1,53)}=2.32$, p=0.13, n=55, Fig S2.2) and therefore samples were considered one group for further analysis. Analysis for both decomposition state and strand method were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S5).

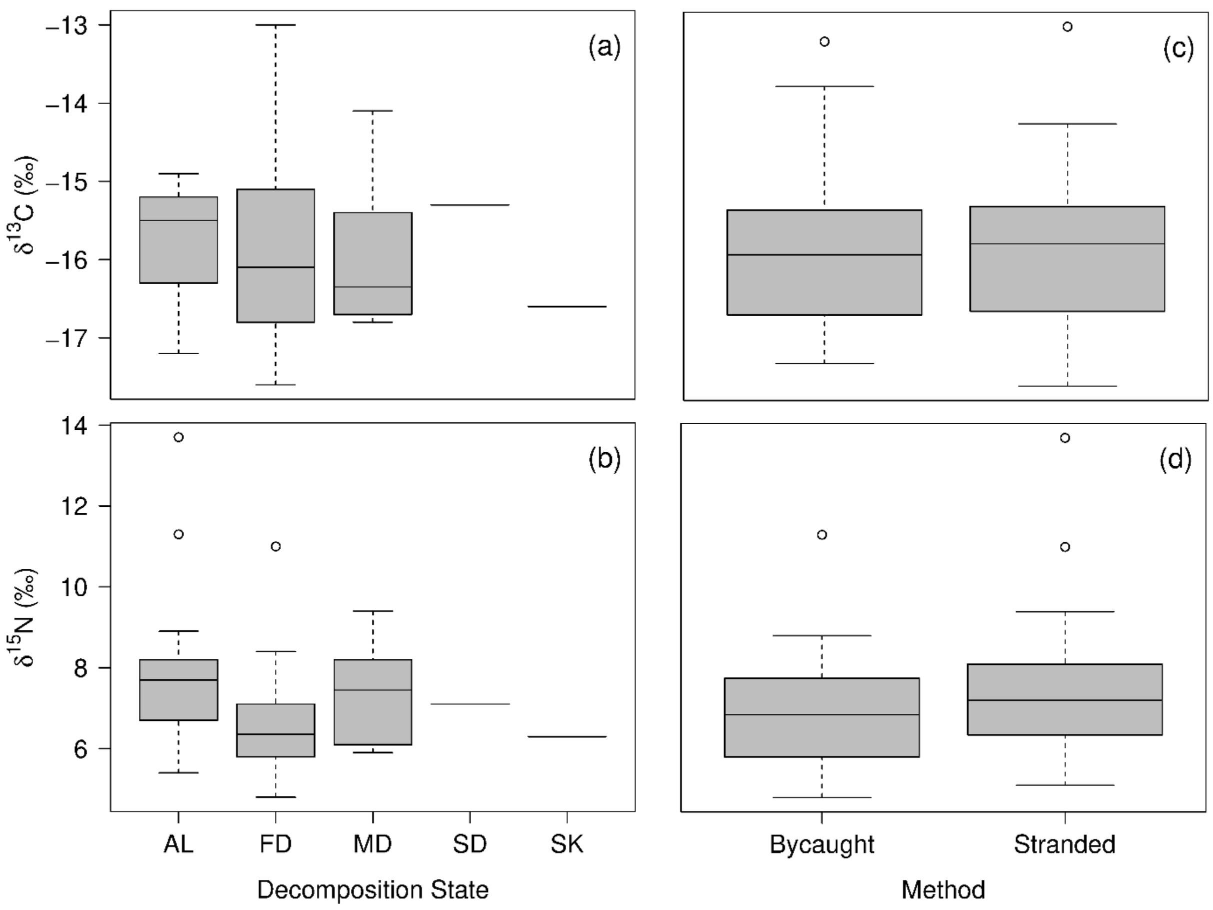

Fig. S2.2 (a) $\delta^{13}C$ and (b) $\delta^{15}N$ values of stranded loggerhead turtles of varying decomposition states found in the North Levantine basin. AL: alive, FD: fresh dead, MD: moderately decomposed, SD: severely decomposed, SK: skeleton. (c) $\delta^{13}C$ and (d) $\delta^{15}N$ values of stranded loggerhead turtles either stranded or bycaught in the North Levantine basin

Appendix S3 – Temporal variation in isotope ratios

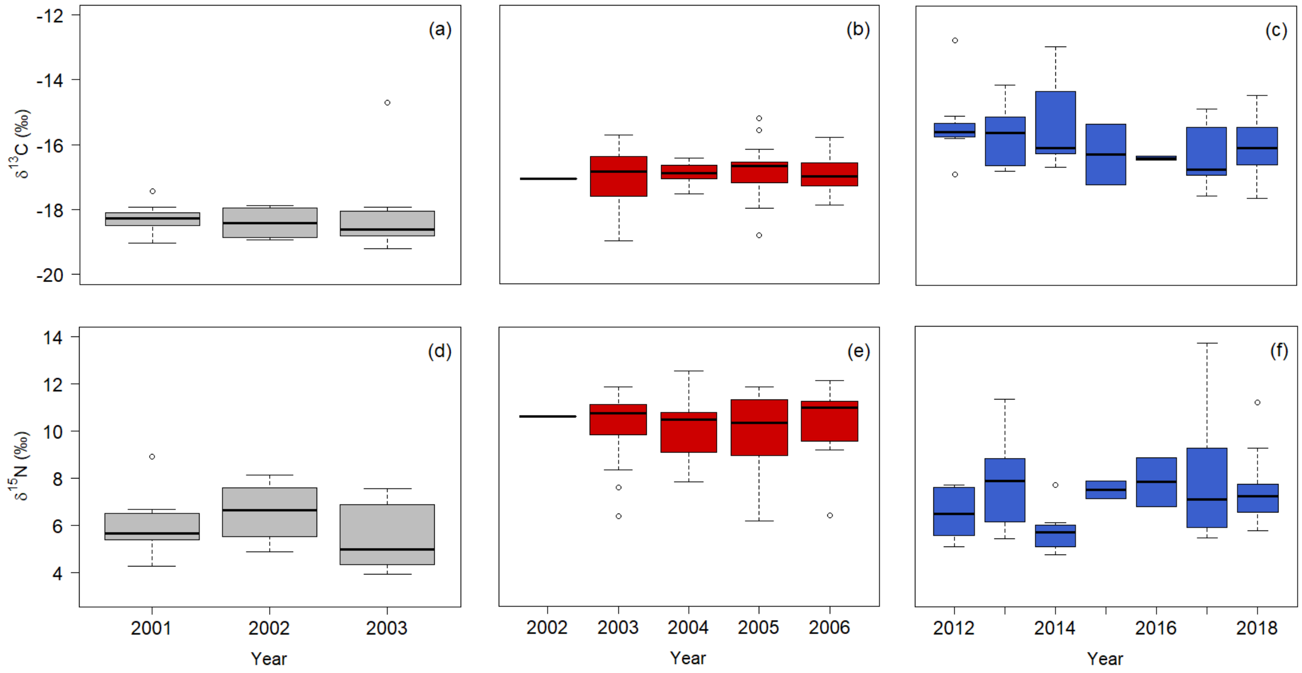

Fig. S3.3 Temporal change of δ^{13}C (top row) and δ^{15}N values (bottom row) of juvenile loggerhead turtles sampled in the Central Mediterranean (a,d), NE Adriatic (b,e), and North Levantine basin (c,f)

Appendix S4 – Seasonal variation in isotope ratios

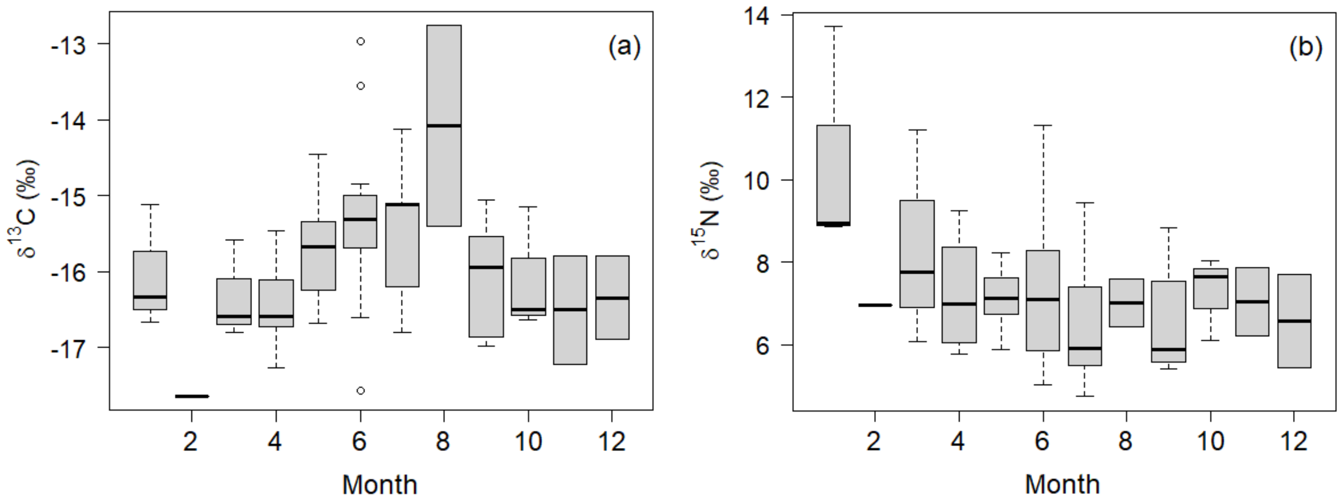

Fig. S4.4 Seasonal change of δ^{13}C and δ^{15}N values of juvenile loggerhead turtles sampled in the North Levantine basin.

Appendix S5 - Sensitivity of the analysis to the isotope analytical uncertainties

To determine the robustness of our isotope analysis each statistical analysis underwent uncertainty analysis. Analytical precision for $\delta^{13}C$ and $\delta^{15}N$ values was 0.18‰ and 0.20‰, respectively, determined as the standard deviation from the reference materials $USGS_{40}$, $USGS_{41}$, and BLS (see Table S5.1 for values). Analytical accuracy was calculated as the sample variance across all samples (see Table S5.1 for values). The combined analytical uncertainty was estimated as a sum of squares of the analytical precision and accuracy assuming that they are uncorrelated (see Table S5.1 for values). Therefore, to identify that the results are insensitive to the isotope combined analytical uncertainties, each analysis was repeated 100 times whilst perturbing the isotope data using additive noise. Noise was calculated as random values following a truncated Gaussian distribution centred on zero with a standard deviation equal to the combined analytical uncertainty. For each analysis the percentage of repeats with a p-value that meets the desired p-value was calculated (see Table S5.1 for values).

Table S5.1 Uncertainty analysis results. % of repeats: percentage of repeats with the desired p-values which are shown in parenthesis. CMed: Central Mediterranean, EIon: East Ionian, NEA: NE Adriatic, NL: North Levantine basin.

Statistical analysis	Isotope ratio	Analytical accuracy (‰)	Analytical Precision (‰)	Combined uncertainty (‰)	% of repeats
Variation in isotope ratios with decomposition state					
	Carbon	0.94	0.18	0.48	100 ($p>0.05$)
	Nitrogen	2.63	0.20	2.64	100 ($p>0.05$)
Variation in isotope ratios with strand method					
	Carbon	1.03	0.18	1.04	100 ($p>0.05$)
	Nitrogen	2.67	0.20	2.68	97 ($p>0.05$)
Inter-sample variation in isotope ratios					
	Carbon	0.14	0.18	0.23	100 ($p>0.05$)
	Nitrogen	0.33	0.20	0.38	100 ($p>0.05$)
Temporal variation in isotope ratios					
CMed	Carbon	0.68	0.18	0.70	100 ($p>0.05$)
	Nitrogen	1.37	0.20	1.39	100 ($p>0.05$)
NEA	Carbon	0.46	0.18	0.50	100 ($p>0.05$)
	Nitrogen	2.05	0.20	2.06	100 ($p>0.05$)
NL	Carbon	1.07	0.18	1.09	100 ($p>0.05$)
	Nitrogen	2.58	0.20	2.59	69 ($p>0.05$)
Seasonal variation in isotope ratios					
	Carbon	0.98	0.18	1.00	100 ($p<0.05$)
	Nitrogen	2.88	0.20	2.89	92 ($p<0.05$)
Variation in isotope ratios with region					
Analysis of Variance	Carbon	0.58	0.18	0.61	100 ($p<0.05$)
	Nitrogen	1.77	0.20	1.79	100 ($p<0.05$)
Analysis of Covariance	Carbon	0.58	0.18	0.61	96 ($p<0.05$)
	Nitrogen	1.77	0.20	1.79	99 ($p<0.05$)
Variation in isotope ratios with sex					
CMed	Carbon	0.65	0.18	0.68	100 ($p>0.05$)
	Nitrogen	1.31	0.20	1.33	91 ($p>0.05$)
NEA	Carbon	0.45	0.18	0.48	94 ($p>0.05$)
	Nitrogen	1.60	0.20	1.61	100 ($p>0.05$)
NL	Carbon	1.05	0.18	1.07	100 ($p>0.05$)
	Nitrogen	1.75	0.20	1.76	99 ($p>0.05$)
Variation in isotope ratios with size					
CMed	Carbon	0.97	0.18	0.99	100 ($p>0.05$)
	Nitrogen	2.69	0.20	2.70	100 ($p>0.05$)
EIon	Carbon	0.97	0.18	0.99	100 ($p>0.05$)
	Nitrogen	2.69	0.20	2.70	100 ($p>0.05$)
NEA	Carbon	0.97	0.18	0.99	86 ($p>0.05$)
	Nitrogen	2.69	0.20	2.70	95 ($p<0.05$)
NL	Carbon	0.97	0.18	0.99	100 ($p<0.05$)
	Nitrogen	2.69	0.20	2.70	100 ($p<0.05$)

CHAPTER 4: SPATIAL ECOLOGY OF LOGGERHEAD TURTLES: INSIGHTS FROM STABLE ISOTOPE MARKERS AND SATELLITE TELEMETRY

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ABSTRACT

Aim Using a combination of satellite telemetry and stable isotope analysis (SIA) our aim was to identify foraging grounds of loggerhead turtles (*Caretta caretta*) at important rookeries in the Mediterranean, examine foraging ground fidelity, and across 25 years determine the proportion of nesting females recruiting from each foraging region to a major rookery in Cyprus.

Location Mediterranean Sea

Methods Between 1993 and 2018, we investigated the spatial ecology of loggerhead turtles from rookeries in Cyprus and Greece using satellite telemetry (n=55 adults) and SIA of three elements (n=296).

Results Satellite telemetry from both rookeries revealed the main foraging areas as the Adriatic region (Cyprus: 4% of individuals, Greece: 55%), Tunisian Plateau (Cyprus: 16%, Greece: 40%), and the eastern Mediterranean (Cyprus: 80%, Greece: 5%). Combining satellite telemetry and SIA allowed 64% of all nesting females to be assigned to; the Adriatic region (Cyprus: 2%, Greece: 38.5%), Tunisian Plateau (Cyprus: 47%, Greece: 38.5%), and the eastern Mediterranean (Cyprus: 51%, Greece: 23%), which are markedly different to proportions obtained using satellite telemetry. The proportion of the Cyprus nesting cohort using each foraging region did not change significantly, with the exception that individuals foraging in the Adriatic region are only present in the Cyprus nesting population from 2012. Repeat satellite tracking (n=3) and temporal consistency in isotope ratios (n=36) of Cyprus females, strongly suggest foraging ground fidelity over multiple decades.

Main Conclusions This study demonstrates the advantages of combining satellite telemetry and SIA to investigate spatial ecology at a population level. The importance of the Tunisian Plateau for foraging is demonstrated. This study indicates that females generally show high fidelity to foraging grounds and shows a potential recent shift to foraging in the Adriatic region for Cyprus females, whilst the importance of other regions persist across decades, thus providing baselines to develop and assess conservation strategies.

Keywords $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$, Foraging ecology, Loggerhead turtle, Mediterranean, Migration, Satellite telemetry, Sea turtle, SIA

INTRODUCTION

Many marine species migrate over long distances, often travelling thousands of kilometres across remote areas, between critical habitats. Consequently, understanding their movements and identifying areas of habitat use can be challenging. Marine migrants are considered particularly vulnerable to overexploitation, habitat loss, and climate change (Robinson et al., 2009) and a lack of knowledge of where and how populations move throughout their life cycle makes it difficult to identify potential risks to their survival. It is therefore necessary to understand the geographical range and migratory connectivity of a species for successful development of long-term conservation plans (Webster et al., 2002).

Marine turtles often migrate across ocean basins between foraging and nesting grounds (e.g. Shillinger et al., 2008), and several geographically distinct foraging areas are typically used by individual nesting populations (e.g. Hays et al., 2006; Seminoff et al., 2008; Stokes et al., 2015; Dujon et al., 2018). Traditionally, conservation, and conservation-driven research, of marine turtles has been focused on easily accessible nesting grounds (Bjorndal et al., 1999; Hamann et al., 2010), protecting nesting females and their eggs, thus potentially only protecting a small proportion of the life cycle of the species. The large geographical range over which marine turtles migrate and forage means that turtles are under high threat from fisheries so require a more diverse approach to conservation (Wallace et al., 2011). Bycatch is one of the key threats to marine turtles in the Mediterranean Sea resulting in high levels of mortality (conservatively 44,000 deaths per year, Casale, 2011; Casale et al., 2018). Consequently, working towards the conservation of critical marine regions, including foraging grounds and migratory routes, is considered a research priority in Mediterranean marine turtle ecology (Casale et al., 2018).

A common technique used in marine megavertebrate spatial ecology is satellite telemetry which enables migratory species to be tracked over long distances (e.g. Gillespie et al., 2001). This can provide fine-scale near real-time movement data on location and speed, but is an expensive technique, and this cost can often limit the sample size (Godley et al., 2008). In contrast, stable isotope analysis (SIA) is a powerful but relatively cheap forensic tool and has been used for several marine taxa (Rubenstein & Hobson, 2004; Newsome et al., 2010; Bird et al., 2018), including marine turtles (Figgener et al., 2019a,b; Haywood et al., 2019), to gain insights into the spatial and foraging ecology of marine species. Combining the locational data of satellite telemetry with stable isotope ratios allows scaling up and has been shown to enable inference of habitat use at a population level (e.g. Bradshaw et al., 2017; Ceriani et al., 2015, 2017). This would enable conservation plans to be better informed, targeting foraging grounds that support the largest proportion of the nesting cohort.

Within low-metabolically active tissues of a consumer, the ratio of stable isotopes reflects the food that an individual has consumed and the location where it was ingested, therefore, acting as intrinsic habitat markers of migratory connectivity (DeNiro & Epstein, 1978). In marine research, the ratio of ^{13}C:^{12}C (expressed as $\delta^{13}C$), ^{15}N:^{14}N (expressed as $\delta^{15}N$), and ^{34}S:^{32}S (expressed as $\delta^{34}S$) are most commonly used as geographical markers. Carbon isotope ratios reflect the primary producer at the base of the food chain in which feeding occurs (DeNiro & Epstein, 1978), with benthic and nearshore regions supported by algae and seagrass exhibiting high $\delta^{13}C$ values in comparison to pelagic and oceanic regions supported by phytoplankton (DeNiro & Epstein, 1978; Graham et al., 2010). Nitrogen isotope ratios of marine primary producers differ in relation to (1) nitrogen-based processes (e.g. nitrification, denitrification, and N_2-fixation), and (2) nitrogen isotope ratios of their nutrient sources (e.g. N_2, ammonium, and nitrate) (Montoya, 2007). Sulphur isotope ratios in primary producers differ based on access to sulphides with inshore ecosystems supported by seagrass and microphytobenthos exhibiting low $\delta^{34}S$ values when compared to offshore ecosystems supported by phytoplankton (e.g. Bradshaw et al., 2017). $\delta^{34}S$ values are believed to be a true habitat marker as they are independent of fractionation from prey to predator, unlike $\delta^{13}C$ and $\delta^{15}N$ values (McCutchan et al., 2003). Despite the benefits of analysing all three isotopes, only one previous study has used this methodology for loggerhead turtles (Tucker et al., 2014). The oligotrophic Mediterranean Sea has regional heterogeneity in salinity, temperature, and primary productivity, all of which influence nutrient cycling (Zotier et al., 1999). Therefore, the Mediterranean can support regions and food webs of differing isotopic compositions, and this variation can allow marine turtle foraging habitats to be inferred (e.g. Cardona et al., 2014; Bradshaw et al., 2017).

Fresh egg yolk and epidermis tissue sampled during the egg laying process are considered representative of the diet consumed in the foraging ground used several months prior to the tissue being sampled (Ceriani et al., 2014). The combination of satellite telemetry and SIA data allows the isotope ratios of specific foraging grounds to be determined. If isotope ratios of foraging grounds are distinct, this enables untracked females to be reliably assigned to putative foraging grounds from a single tissue sample, hence providing an understanding of the spatial ecology at a population level (e.g. Seminoff et al., 2012; Ceriani et al., 2015). In addition, the temporal consistency of isotope ratios have been used for confirming foraging ground fidelity in marine taxa (e.g. Newsome et al., 2010), including marine turtles (e.g. Thomson et al., 2012; Bradshaw et al., 2017). If foraging ground fidelity occurs, then long-term studies enable the proportion of individuals in each annual nesting cohort using each foraging ground to be determined across multiple nesting seasons and therefore identifying potential shifts in population dynamics (e.g. Ceriani et al., 2015, 2017; Bradshaw et al., 2017). Temporal changes in the proportion of individuals using each foraging ground could be inferred as changes in the foraging ground dynamics, including changes in recruitment, survival of individuals, or changes in foraging resources and environmental conditions. These could in turn be reflective of natural ecological or anthropological changes.

It is estimated that there are approximately 16,000 adult loggerhead turtles in the Mediterranean of which ~3500 females nest annually (Casale & Heppell, 2016). The major foraging regions for these nesting females have been identified using flipper tag returns and satellite telemetry and include the northern Adriatic Sea, Aegean Sea, Turkey, Egypt, and the Tunisian Plateau (Godley et al., 2003; Lazar et al., 2004; Broderick et al., 2007; Hays et al., 2010, 2014; Zbinden et al., 2008, 2011; Margaritoulis & Rees, 2011; Schofield et al., 2013; Patel et al., 2015; Snape et al., 2016; see also reviews by Margaritoulis et al., 2003; Luschi & Casale, 2014; Casale et al., 2018). However, this information currently exists for only a small sample of these populations. Nest counts in Mediterranean rookeries are generally not increasing as rapidly as expected despite intensive conservation efforts on the nesting beaches (Casale et al., 2018). A more comprehensive picture of where Mediterranean loggerhead turtles are foraging would help target conservation strategies (Casale et al., 2018). Combining satellite telemetry and SIA, Bradshaw et al. (2017) described in detail the foraging grounds of a large proportion of nesting green turtles (*Chelonia mydas*) from an important rookery in North Cyprus. We aimed to replicate this study, and be the first to analyse three isotope markers for loggerhead turtles in the Mediterranean, to identify the foraging grounds used by loggerhead turtles from nesting populations in Greece and North Cyprus, examine the level of foraging ground fidelity, and determine the proportion of the North Cyprus nesting cohort using each identified foraging ground during this multi-decadal study.

METHODS

2.1 FIELD DATA AND SAMPLE COLLECTION

The beaches at Alagadi (35°20'N, 33°29'E) are major nesting grounds for loggerhead turtles in North Cyprus (Casale et al., 2018), where nest protection and monitoring has been implemented since 1992 (Broderick et al., 2002, Fig. 1). Nightly monitoring (for details see Stokes et al., 2014) took place between 20:30 and 05:00 during the nesting seasons between 1993 and 2018, from May to mid-August. For individual identification, after laying, females had flipper tags placed in the trailing edge of both fore-flippers and, since 1997, passive integrated transponders were injected into the shoulder muscle. Minimum curved carapace length (CCL, notch-to-notch, Bolten et al., 1999) was measured with a flexible measuring tape as an indicator of body size.

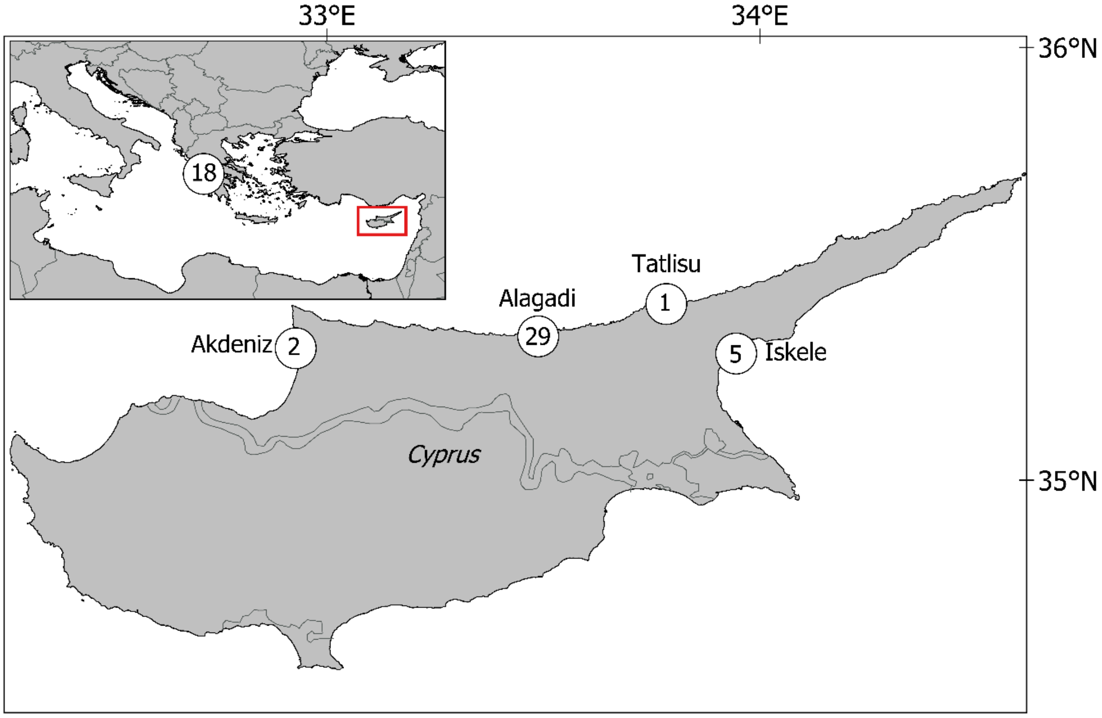

Figure 1 Location of loggerhead turtle satellite tracking deployment sites in North Cyprus (n = 4 sites). Insert box shows the location of Cyprus and the deployment site Zakynthos, Greece (from Zbinden et al. (2011)). Number of satellite tags deployed indicated within circles at each area.

2.2 SATELLITE TELEMETRY

At Alagadi Beach, between 2001 and 2018, 32 Platform Terminal Transmitters (PTTs) were attached to 29 adult female loggerhead turtles after oviposition, with three of these individuals tracked on two occasions. In addition, eight PTTs were deployed from other beaches in North Cyprus; Akdeniz (35°20'N, 32°56'E), Iskele (35°16'N, 33°55'E), and Tatlisu (35°41'N, 33°76'E, Fig. 1, see Appendix S1 in Supporting Information). The PTTs deployed between 2001 and 2012 from North Cyprus were previously published (Godley et al., 2003; Broderick et al., 2007; Snape et al., 2016), whilst 11 PTTs were attached in 2017-2018 on Alagadi (see Appendix S1). To further increase sample sizes, previously published satellite telemetry data for 18 individuals nesting at the Bay of Laganas on Zakynthos, Greece (37°72'N, 20°86'E, Zbinden et al., 2008, 2011) were included in our analysis (Fig. 1, see Appendix S1 in Supporting Information). For details on the analysis of satellite telemetry data see Appendix S1.

2.3 STABLE ISOTOPE ANALYSIS

Of 373 individual females that were recorded nesting at Alagadi between 2001 and 2018, epidermis tissue samples ($<0.000025\ m^2$) were collected using a scalpel from the trailing edge of the right fore-flipper (from the third membrane) or the shoulder (between the neck and fore-flipper) from 233 individuals (21 of which were satellite tracked individuals). Until required for analysis, tissue samples were stored in either, >70% ethanol at room temperature (n=421), >70% ethanol in a non-frost-freezer (n=31), or frozen in sodium chloride solution (n=28). Dermis tissue was separated from the skin samples in the laboratory and only the epidermis tissue was used in the analysis. For details on the stable isotope analysis conducted, see Appendix S2 in Supporting Information.

Several individuals were sampled multiple times to determine the consistency of isotope ratios between left and right flipper samples (n=38 females), between flipper and shoulder samples (n=51 females), across successive clutches in the same season (sampled during first encounter and 10-16 days after the previous clutch, n= 30 females), and across nesting seasons (n=36 females). For details on the methods of this analysis see Appendix S2 in Supporting Information.

In addition, stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) were available for the present study from 12 satellite tracked (see Appendix S1) and 51 untracked females from Zakynthos (previously published in Zbinden et al., 2011). Zbinden et al. (2011) collected yolk from unhatched eggs (during post-hatchling clutch excavation) and fresh eggs (during laying). Yolk samples were frozen and subjected to lipid extraction. Therefore, to obtain comparable values to the present study, we converted the isotope ratios of unhatched yolk to fresh yolk (by subtracting 0.49 ‰ from $\delta^{15}N$ values, see Zbinden et al., 2011) and then to epidermis values using published tissue conversion equations for frozen fresh lipid extracted yolk to female loggerhead turtle epidermis values ($\delta^{13}C_{epi}=0.90*\delta^{13}C_{yolk}-0.95$, $\delta^{15}N_{epi}=1.05*\delta^{15}N_{yolk}-0.75$, Kaufman et al., 2014).

2.4 FORAGING GROUND ASSIGNMENT

Tissue samples were available for 21 Alagadi and 12 Zakynthos satellite tracked females. Due to limited tissue quantity, six Alagadi individuals could only be run for $\delta^{13}C$ and $\delta^{15}N$ analysis, whilst 15 were analysed for all three stable isotope ratios (see Appendix S1). $\delta^{13}C$ and $\delta^{15}N$ analysis were prioritised for comparison to previous SIA research, as only four marine turtle studies to date have analysed $\delta^{34}S$ values (see review by Haywood et al., 2019). From the previous study only $\delta^{13}C$ and $\delta^{15}N$ values were available from Zakynthos individuals. The PTTs of two Alagadi individuals ceased to function during migration, therefore these were excluded from further analysis.

To enable assignment of untracked females to putative foraging grounds, statistically significant differences in stable isotope ratios among foraging grounds are required. To determine suitable geographical regions which are isotopically distinct a Principal Component Analysis was run, and an Analysis of Covariance was used to confirm if the isotope ratios of the identified regions were significantly different from each other. For details of this analysis see Appendix S3 in Supporting Information. To assign untracked females to putative foraging grounds, the nominal assignment approach of Linear Discriminant Function Analysis (LDA) was used in the R-package ‘MASS’ (Venables & Ripley, 2002). Non-uniform priors based on the number of turtles tracked to each foraging region were used as recommended by Vander Zanden et al. (2015). As no Zakynthos individuals and not all Alagadi individuals had associated $\delta^{34}S$ values, two LDAs were run. The first for $\delta^{13}C$ and $\delta^{15}N$ values whilst the second included all three isotopes. For the LDA using $\delta^{13}C$ and $\delta^{15}N$ values, the isotope ratios of 31 tracked females (Alagadi: n=19; Zakynthos: n=12) were used as the training dataset to develop the discriminant functions, whilst the remaining 265 untracked females (Alagadi: n=214; Zakynthos: n=51) were the test dataset for assignment to putative foraging grounds. For the LDA using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values (using only Alagadi individuals), the training dataset consisted of 11 tracked females, whilst 160 untracked females were the test dataset for assignment. A jack-knifed leave-one-out cross validation method was used to assess the accuracy of the assignments. Assignments with posterior probabilities of ≥80% were considered successful.

2.5 FORAGING GROUND FIDELITY

Thirty-six individuals that had multi-year $\delta^{13}C$ and $\delta^{15}N$ values, and of those 23, individuals had multi-year $\delta^{34}S$ values, allowed foraging ground fidelity to be examined for this population. Twenty-two individuals had isotope ratios for two nesting seasons, eight for three seasons, three for four seasons, and three for five nesting seasons. To test isotope temporal consistency, repeatability estimates using a linear mixed-effects model for Gaussian data fitted with restricted maximum likelihood were used in the R-package ‘rptR’ (Stoffel et al., 2017). Turtle ID was set as the grouping factor.

2.6 ANNUAL CONTRIBUTIONS TO THE ALAGADI NESTING COHORT

Satellite tracked individuals, with known foraging region, and individuals assigned to putative foraging regions (with posterior probabilities of ≥80%) were used to estimate the proportion of the annual cohort using each foraging ground through SIA. Tissue samples were only collected from 2001 onwards but some individuals, that were identified from 1993 onwards, had samples collected in later seasons and therefore could be assigned to foraging grounds based on the assumption of foraging ground fidelity. To determine whether the proportion of nesters using each foraging ground differed among years (1993 to 2018), generalised additive models for binomial data were run for each foraging ground in the R-package ‘mgcv’ (Wood, 2017), which took autocorrelation into account. All analyses were performed with the software R 3.5.1 (R Core Team, 2018) and for statistical tests, the significance level was alpha = 0.05.

RESULTS

SATELLITE TELEMETRY

From this study a total of 40 PTTs were deployed on 37 females from four release sites in North Cyprus (three females were tracked twice from Alagadi, Figure 1). Locational data were transmitted for 6-2007 days (mean: 371 days). Of these, 37 PTTs provided location data throughout the post-nesting migration to the foraging grounds. From Zakynthos, 18 females were satellite tracked and all transmitted to confirmed foraging grounds and transmitted for 114-740 days (mean: 328 days). Satellite tracked females from North Cyprus had mean CCL of 0.73 ± 0.06 m (range: 0.65 to 0.85 m), whilst turtles from Greece had mean CCL of 0.84 ± 0.04 m (range: 0.76 to 0.89 m). These CCL values are within the ranges recorded for nesting females at each representative site, showing satellite tracked females represent the parent population well (Omeyer et al., 2017; Casale et al., 2018).

Post-nesting females from North Cyprus migrated via numerous migratory routes to the Aegean Sea, the Adriatic region (including the Adriatic Sea and the Gulf of Amvrakikos), and across a large extent of the eastern Mediterranean basin, to foraging grounds in Italy, Turkey, Cyprus, Syria, Lebanon, Israel, Egypt, Libya, Tunisia, and the Tunisian Plateau (Fig. 2a). Females nesting in Greece migrated to Croatia, Slovenia, Italy, Greece, Tunisia, and the Tunisian Plateau (Fig. 2b). Thirty nine females remained in distinct foraging grounds all located on the continental shelf (within the 200 m isobath), fourteen females showed over-wintering behaviours moving to a second distinct area during the winter months, and two turtles (Turtle 21 and Turtle 27) conducted oceanic foraging throughout their deployments in waters >200 m (466 and 222 days, respectively, Fig. 2a). These oceanic individuals were considered untracked for foraging ground assignment as they did not occupy a distinct foraging ground.

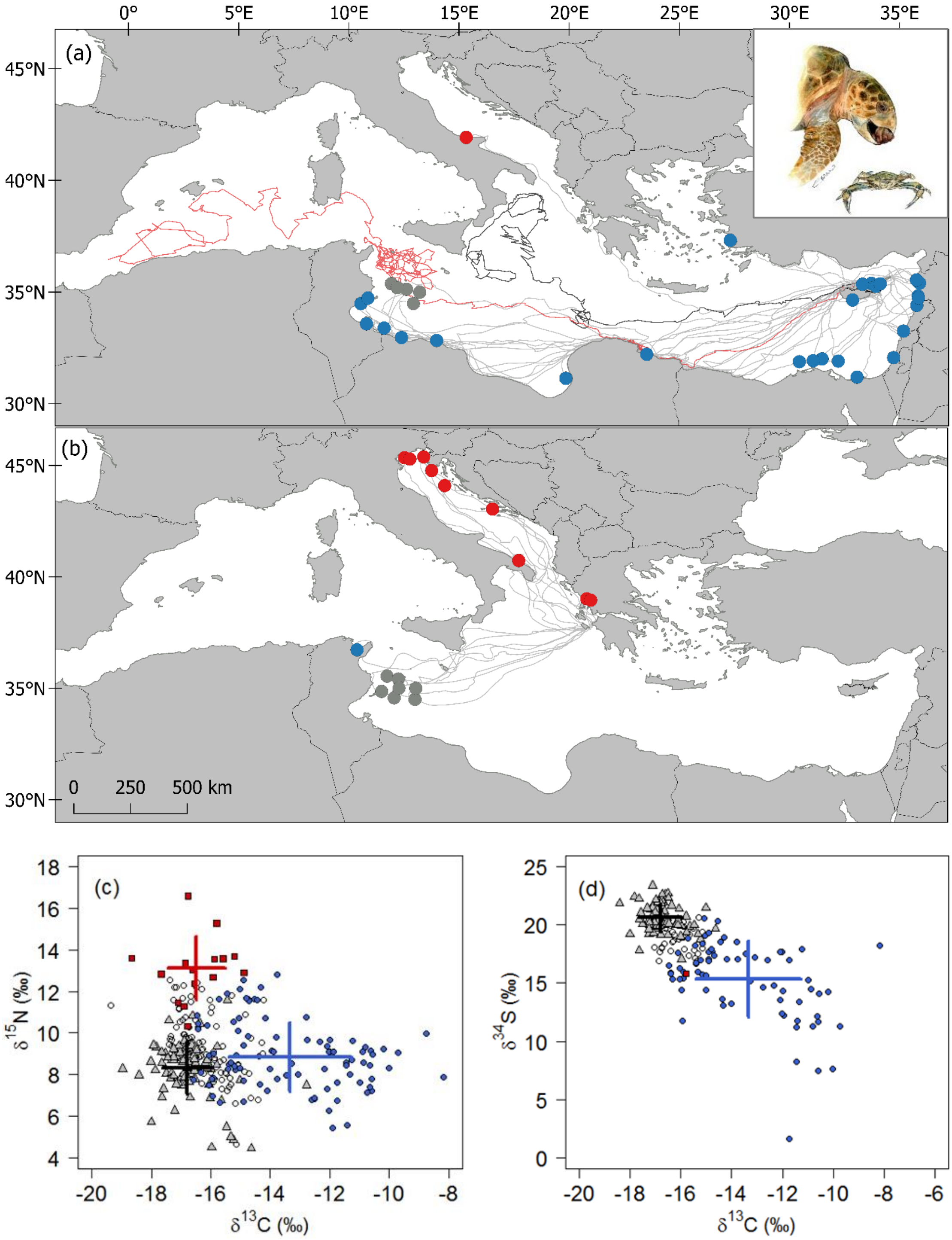

Figure 2 Foraging grounds of female loggerhead turtles tracked from (a) North Cyprus and (b) Greece to the Adriatic region (red), the Tunisian Plateau (grey), and the rest of the eastern Mediterranean (blue). Oceanic movements of Turtle 21 (red) and Turtle 27 (black) are highlighted. (c) bivariate plot of δ^{13}C and δ^{15}N, and (d) δ^{13}C and δ^{34}S, respectively, of loggerhead turtles satellite tracked or isotopically assigned to the Adriatic region (n=15, red squares), the Tunisian Plateau (n=87, grey triangles), or the rest of the eastern Mediterranean (n=92, blue circles). Unassigned individuals = open circles (n=100). Crosses = mean ±SD of each foraging region. Artwork inset of a foraging loggerhead turtle.

3.2 FORAGING GROUND ASSIGNMENT

The Principal Component Analysis identified three isotopically distinct geographical regions (see Appendix S3a in Supporting Information), the Adriatic region, the Tunisian Plateau, and the rest of the eastern Mediterranean (Fig. 2). The ‘Adriatic region’ includes all individuals foraging in the Adriatic Sea and the North Ionian Sea (including the Gulf of Amvrakikos), the ‘Tunisian Plateau’ includes all individuals foraging offshore the Tunisian coast (mean distance from coast: 68.5 km) on the Tunisian Plateau, and the ‘rest of the eastern Mediterranean’ includes all individuals foraging in neritic regions in the eastern Mediterranean basin, including individuals foraging nearshore on the Tunisian Plateau (Fig. 2). These regions had significantly different isotope ratios even when body size was taken into account (Analysis of Covariance, $\delta^{13}C$: $F_{2,25}$= 11.99, p<0.001, $\delta^{15}N$: $F_{2,25}$=14.62 , p<0.001, $\delta^{34}S$: $F_{2,7}$= 4.47, p=0.05, see Appendix S3b). A post hoc Tukey’s Honest Significant Difference test revealed that significant differences occurred between all regions with the Adriatic region distinct based on high $\delta^{15}N$ values, the Tunisian Plateau distinct based on high $\delta^{34}S$ values, and the rest of the eastern Mediterranean distinct based on high $\delta^{13}C$ values (see Appendix S3a).

Tissue samples were available from 265 untracked females (of which 51 were from Greece), which ranged in size between 0.59 to 0.94 m (mean: 0.722 m). Stable isotope ratios ranged from -19.37 to -8.18 ‰ for $\delta^{13}C$ (mean: -15.47 ‰), 4.44 to 12.8 ‰ for $\delta^{15}N$ (mean: 8.88 ‰), and 1.62 to 23.39 ‰ for $\delta^{34}S$ (mean: 18.05‰). The LDA using $\delta^{13}C$ and $\delta^{15}N$ values correctly assigned 74% of satellite tracked individuals to their foraging region (Alagadi: 69% and Zakynthos: 83%) as tested by the jack-knifed leave-one-out cross validation method. The LDA using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values correctly assigned 73% of the Alagadi satellite tracked females (Zakynthos individuals did not have associated $\delta^{34}S$ values so were not included). The resultant uncertainties in the LDA due to propagating the isotope analytical uncertainties are ±0.1% (for both cases, for details on this analysis see Appendix S5 in Supporting Information).

Untracked individuals included in both LDAs (n=129) were assigned to the same foraging region, showing consistency in this method. For Alagadi 70% of untracked females (n= 148) were successfully assigned to putative foraging grounds. Of those assigned, 2% were assigned to the Adriatic region, 47% to the

Tunisian Plateau, and 51% to the rest of the eastern Mediterranean. For Zakynthos 25% of untracked females (n= 13) were successfully assigned to putative foraging grounds. Of those assigned, 38.5% were assigned to the Adriatic region, 38.5% to the Tunisian Plateau, and 23% to the rest of the eastern Mediterranean. Due to posterior probabilities being ≤80%, 30% of untracked Alagadi females (n = 62) and 75% of untracked Zakynthos females (n = 38) remained unassigned (Fig. 2, see Appendix S3a). Oceanic Turtle 27 was assigned to the Tunisian Plateau, whilst Turtle 21 was unassigned due to posterior probabilities being ≤80%. Isotope ratios of satellite tracked and isotopically assigned females are shown in Table S3.2 in the Supporting Information.

3.3 FORAGING GROUND FIDELITY

Three individuals (Turtles 1, 3, and 37) were tracked during two foraging seasons and showed strong foraging ground fidelity. The centroids of their foraging grounds were separated by 1.2 km (Turtle 1), 20.2 km (Turtle 3), and 0.2 km and 0.8 km (Turtle 37, Fig. 3). Turtle_37, was tracked for 2007 days across two foraging seasons, and shuttled repeatability between two foraging grounds 13 km apart but showed exceptionally high fidelity to both foraging grounds (Fig. 3). For individuals sampled for SIA, the $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values across multiple nesting seasons had highly significant repeatability estimates (Repeatability estimation (R), $\delta^{13}C$: R ± Standard error=0.92 ± 0.02, 95% Confidence Interval=0.86 − 0.95, $p<0.001$, n=36, $\delta^{15}N$: R ± Standard error=0.94 ± 0.02, 95% Confidence Interval=0.89 − 0.96, $p<0.001$, n=36, $\delta^{34}S$: R ± Standard error=0.84 ± 0.06, 95% Confidence Interval=0.68 − 0.92, $p<0.001$, n=23, Fig. 4). The analysis was repeated 100 times whilst perturbing the isotope data using additive noise (with a noise distribution based on the analytical uncertainties). In all cases the p-values remained < 0.05 (for details of this analysis see Appendix S5 in Supporting Information). Therefore, these results are considered to be insensitive to the isotope analytical uncertainties. Isotope ratios of the oceanic Turtle 21 did not differ between two nesting seasons despite not occupying a distinct foraging ground (Fig. 4, only one sample was available for the oceanic turtle Turtle 27).

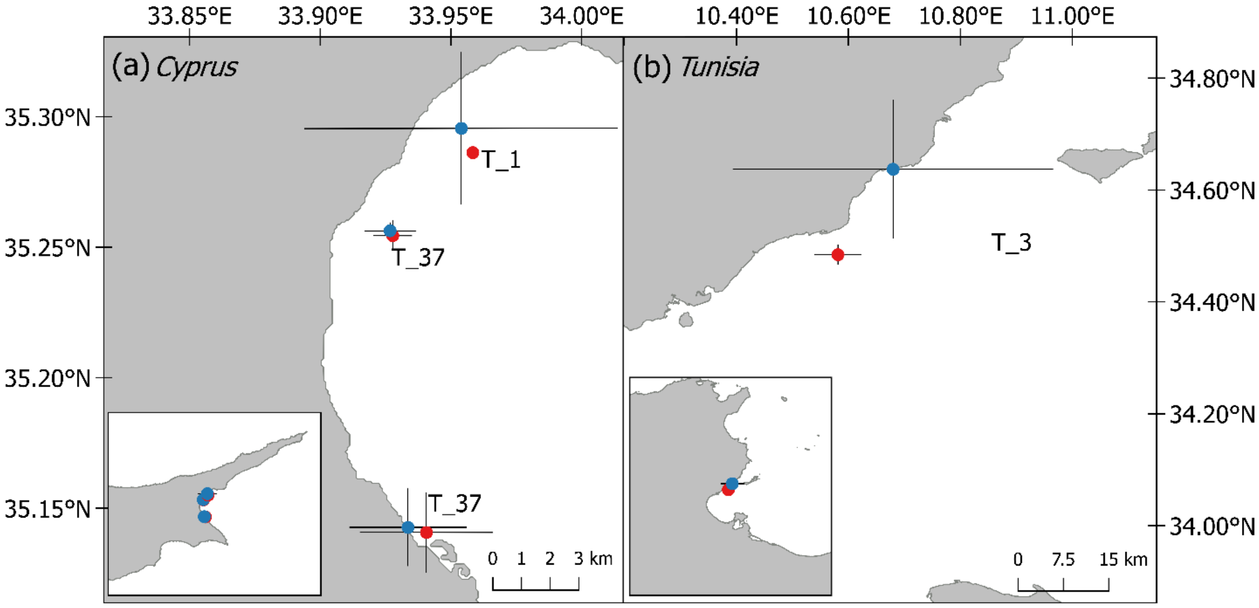

Figure 3 Foraging ground fidelity of three female loggerhead turtles tracked during two foraging seasons from Alagadi Beach, North Cyprus. (a) Foraging grounds of Turtle 1 (T_1) and Turtle 37 (T_37) located on the east coast of North Cyprus. Turtle 37 shuttled repeatability between the two foraging grounds shown throughout the seasons. (b) Foraging grounds of Turtle 3 (T_3) located on the east coast of Tunisia. Points = foraging ground centroids (blue = first foraging season, red = second foraging season), crosses = standard deviations. Insert box shows the location of (a) and (b).

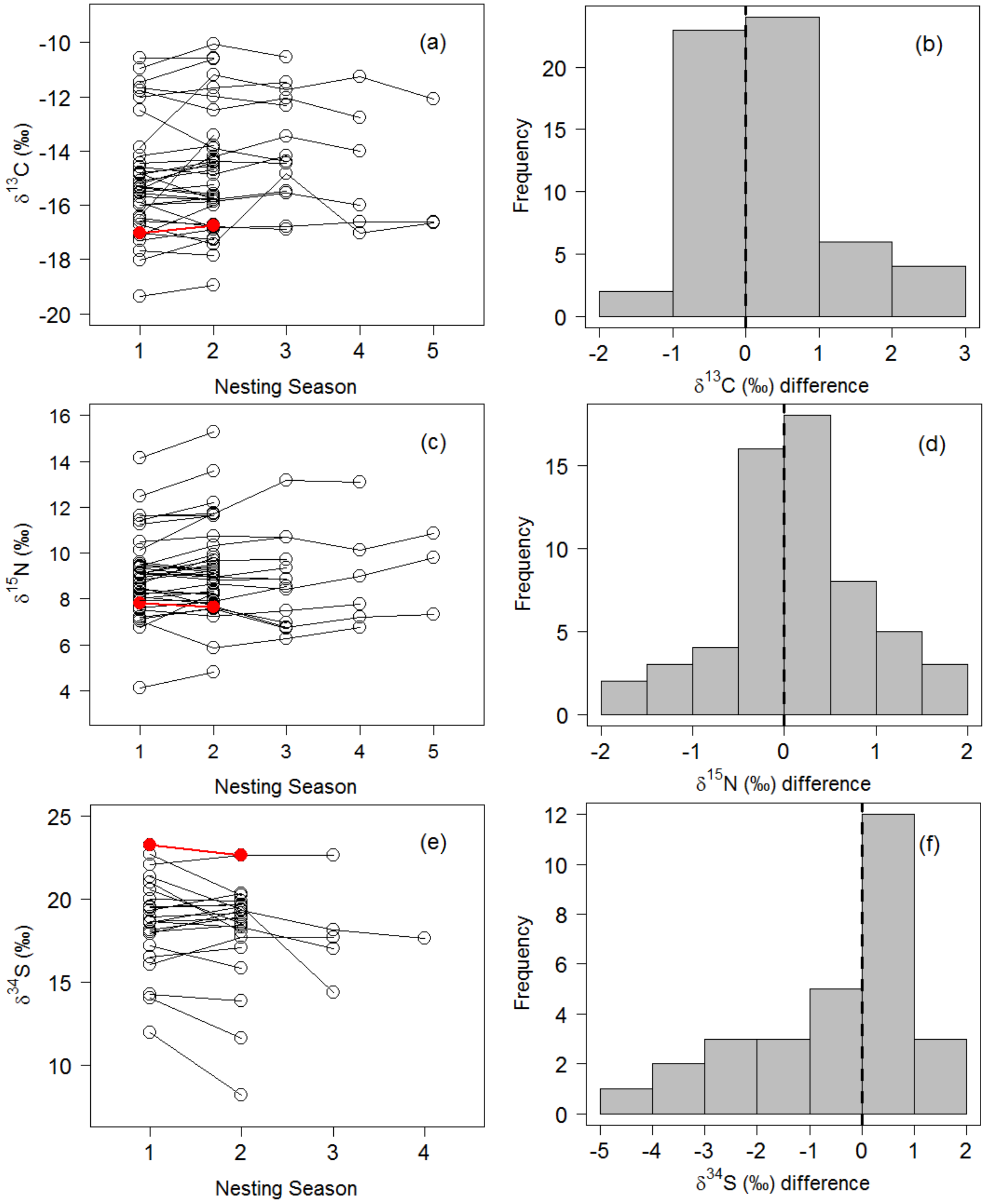

Figure 4 (a), (c), and (e) show temporal consistency in δ^{13}C, δ^{15}N, and δ^{34}S values of samples collected from female loggerhead turtles across multiple nesting seasons in Alagadi Beach, North Cyprus. The oceanic Turtle 21 is highlighted in red. (b), (d), and (f) show differences in isotope ratios between samples using the first nesting season as a reference.

3.4 ANNUAL CONTRIBUTIONS TO THE ALAGADI NESTING COHORT

Across the study period 70% (n=148) of sampled Alagadi nesting females were successfully assigned to a putative foraging region. Of these, fewest females foraged in the Adriatic region (2%) whereas the remainder were approximately equally split between the Tunisian Plateau (47%) and the rest of the eastern Mediterranean (51%). By determining foraging ground use at a population level, this study shows the number of females utilising each region is markedly different to the proportions obtained from using purely the satellite tracking data, which results in one Alagadi individual tracked to the Adriatic region (4%), four to the Tunisian Plateau (16%), and 20 to the rest of the eastern Mediterranean (80%, see Appendix S1 in Supporting Information). Of those assigned to the Adriatic region, half were remigrants (returning females), whilst 26% of Tunisian Plateau foragers and 29% of the foragers in the rest of the eastern Mediterranean were remigrants. The proportion of individuals assigned to all foraging regions did not differ among years (Generalised additive model, Adriatic region: t-value=0.21, df=25, p=0.83, Tunisian Plateau: t-value=0.97, df=25, p=0.34, rest of the eastern Mediterranean: t-value=0.44, df=25, p=0.67, Fig. 5, for the number of females assigned to each foraging ground see Table S4.3 in the Supporting Information) but it should be noted that breeding individuals that use the Adriatic region were only recorded from 2012 onwards.

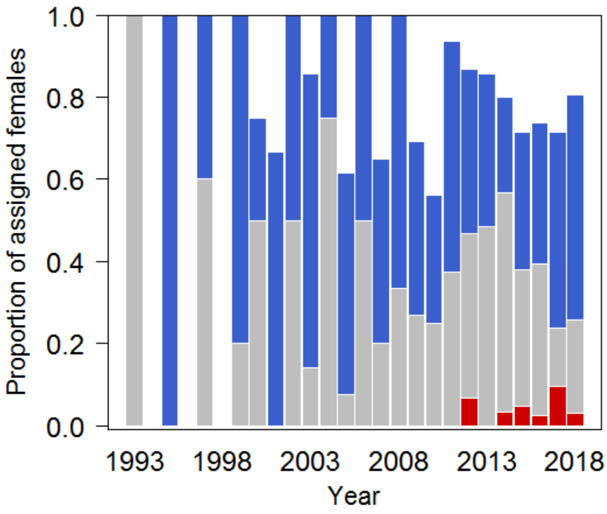

Figure 5 Proportion of the Alagadi (North Cyprus) annual loggerhead turtle nesting cohort assigned to the Tunisian Plateau (grey), the rest of the eastern Mediterranean (blue), or the Adriatic region (red).

DISCUSSION

This study adds to the growing body of literature that demonstrates the benefits of combining the complementary methodological approaches of satellite telemetry and SIA in understanding the spatial ecology of animal populations (e.g. Ceriani et al., 2012; Seminoff et al., 2012; Reich et al., 2017; for a review and references therein see Haywood et al., 2019). This combined approach allowed us to understand the importance of foraging grounds for the broader population, which demonstrates a remarkable difference from results obtained from several individuals using satellite telemetry alone. When teamed with long-term individual-based monitoring programmes these combined techniques can determine whether the importance of these foraging regions persist over decades and provide baselines to assess future conservation strategies (e.g. Pajuelo et al., 2012; Vander Zanden et al., 2014; Ceriani et al., 2015, 2017; Bradshaw et al., 2017).

Previous satellite telemetry has shown these North Cyprus and Greece nesting populations utilise a broad range of foraging grounds (Godley et al., 2003; Broderick et al., 2007; Hays et al., 2010, 2014; Zbinden et al., 2008, 2011; Schofield et al., 2013; Snape et al., 2016). The PTTs deployed in this study in 2017 and 2018 (see Appendix S1) continued to identify a wide range of migratory routes and new foraging grounds including the first use of the Aegean Sea, the Adriatic Sea, and the western Mediterranean basin, none of which had previously been observed for the North Cyprus nesting population (Fig. 2a). Satellite telemetry results suggest the majority of the Alagadi nesting population forages around the eastern Mediterranean Basin (80%), whilst few forage on the Tunisian Plateau (16%) and in the Adriatic region (4%). However, by combining telemetry results with the powerful forensic tool of SIA, this study identifies the importance of the Tunisian Plateau as a foraging region for this population. This region appears to support almost half of the Alagadi nesting population (47%), despite being a relatively small geographical region and is a considerable distance from the rookery (2500 km). This result can be used to better inform conservation, suggesting this relatively small foraging region, which supports a large proportion of the nesting cohort, is targeted for future management.

Prior satellite tracking and SIA studies have also shown the Tunisian Plateau to be a major foraging ground for loggerhead turtle rookeries across the

Mediterranean Sea (e.g. Hays et al., 2010; Zbinden et al., 2011; Schofield et al., 2013; Cardona et al., 2014; Snape et al., 2016) as well as for male (Casale et al., 2013; Schofield et al., 2013; Hays et al., 2014) and juvenile loggerhead turtles (Casale et al., 2012). In addition, both our satellite telemetry and SIA results support previous work showing foraging ground fidelity occurs in this species (Fig. 3 and Fig.4, Broderick et al., 2007; Schofield et al., 2010; Thomson et al., 2012; Tucker et al., 2014). In comparison to satellite telemetry alone, using isotope ratios to investigate foraging site fidelity not only enhances the sample size but enables tracking over decades. This is the first loggerhead turtle study to use this method on multi-decadal data showing foraging site fidelity across five nesting seasons. Isotopically tracking individuals over decades provides a baseline to potentially investigate shifts in habitat use as well as to provide pre- and post-disaster information (e.g. Reich et al., 2017).

In the Mediterranean Sea, bycatch is one of the most important threats to marine turtles and the Tunisian Plateau has some of the highest rates (Casale et al., 2007, 2018; Casale, 2011). In Alagadi and Zakynthos, nest counts are not increasing as rapidly as expected (Casale et al., 2018), suggesting that alternative conservation approaches are needed. This study supports the need to focus site-specific conservation strategies on anthropogenic activities (such as fishing) to key marine habitats, such as the Tunisian Plateau, which may dramatically increase the survival of individuals in this foraging ground and aid in the recovery of many loggerhead rookeries across the Mediterranean. Potential future conservation management approaches to reduce bycatch in important foraging areas, such as the Tunisian Plateau, have been reviewed in Casale et al. (2018). The review highlights the need of monitoring and reporting bycatch, the enforcement of changes to less detrimental fishing gears, as well as mitigation measures such as the use of turtle excluder devices by bottom trawlers or ‘circle hooks’ by longliners (Casale et al., 2018 and references therein).

Both satellite telemetry and SIA show the Adriatic region is a more important foraging area for those nesting in Greece than nesting females in North Cyprus. The use of the Adriatic region by nesting populations in Greece (Lazar et al., 2004; Zbinden et al., 2011; Schofield et al., 2013; Cardona et al., 2014; Hays et al., 2014) and the limited use by eastern nesting populations, such as North Cyprus, have been previously reported (Snape et al., 2016 Margaritoulis & Rees, 2011). Hatchling dispersal studies suggest adult foraging grounds may be selected based on the passive dispersion of hatchlings by surface currents, with those originating from Greece dispersed to the Adriatic region (Hays et al., 2010; Casale & Mariani, 2014), whilst those from eastern nesting sites are restricted from entering this region (Casale & Mariani, 2014). Therefore, with the importance of foraging grounds likely to differ between nesting populations, this study should be replicated for all major nesting grounds to ensure all critical marine habitats for this species are considered in conservation plans.

Temporal differences in hatchling dispersal have been simulated and are thought to be due to fluctuations in surface currents (e.g. Hays et al., 2010). With shifts in ocean circulation likely with future climate scenarios (Hoegh-Guldberg & Bruno, 2010), shifts in hatchling dispersal and in turn adult foraging grounds may occur (Hays et al., 2010). Shifts in foraging grounds will not only determine the potential of fisheries interactions due to variable bycatch rates across the Mediterranean (Casale, 2011) but could also influence reproductive output, with individuals foraging in areas of high productivity, such as the Adriatic region, being larger with larger clutch sizes (e.g. Cardona et al., 2014).

Collecting long-term individual-based data at easily accessible nesting beaches can allow monitoring of shifts in the importance of foraging grounds (e.g. Ceriani et al., 2015, 2017; Bradshaw et al., 2017). Although loggerhead turtle foraging grounds have been identified, how each foraging ground contributes to a nesting cohort on a long-term scale has not been investigated in the Mediterranean and no marine turtle study has investigated this over multiple decades. This study shows that the proportion of the Alagadi cohort using each foraging region did not significantly differ across this multi-decadal study. This suggests little shift in the importance of these regions, with recruitment, survivorship, and conditions potentially remaining similar. In contrast, significant shifts in the relative contributions to foraging grounds has been reported in major loggerhead turtle rookeries in the Atlantic (Pajuelo et al., 2012; Vander Zanden et al., 2014; Ceriani et al., 2017).

Over this 25 year study period, individuals foraging in the Adriatic region were only seen in the Alagadi nesting cohort from 2012 onwards (Fig. 5) and could suggest differences in recruitment and survivorship in some areas or a range shift possibly due to climatic variations in the environmental conditions or anthropological changes (Casale et al., 2018). We support the recommendation by Ceriani et al. (2017) that multi-decadal studies are required to detect long-term trends in population dynamics, providing a baseline to assess temporal shifts in foraging ground importance enabling conservation management to be adapted and targeted appropriately. It also provides baselines to develop and assess future conservation strategies.

This is the first instance of oceanic foraging behaviours reported for the North Cyprus nesting population (Fig. 2a), however, this behaviour has occasionally been recorded previously for adult females in other regions of the Mediterranean Sea (e.g. Bentivegna, 2002; Schofield et al., 2010; Zbinden et al., 2008). Despite oceanic foraging, Turtle 21 showed temporal consistency in isotope ratios (Fig 4) suggesting they are consuming similar prey items from similar food chains across years. Oceanic foraging could reduce the accuracy of using SIA for foraging ground assignment as foraging ground fidelity is required, however, a small proportion of females are doing this. Both oceanic foragers were relatively small in comparison to the other satellite tracked females. A size difference between foraging strategies has been reported in previous SIA studies investigating neritic versus oceanic foragers and was attributed to sparsely distributed planktonic prey in oceanic habitats leading to smaller individuals in comparison to those foraging on nutritional neritic prey (Hatase et al., 2002; Eder et al., 2012; Cardona et al., 2017).

Oceanic Turtle 21 spent 230 days in the Strait of Sicily before entering the western Mediterranean basin. This is the first report of a westerly migration for the North Cyprus nesting population. Although juvenile loggerhead turtles originating from the eastern Mediterranean have been previously reported to forage in the western basin (e.g. Margaritoulis et al., 2003), few adults have been observed to migrate here (e.g. Margaritoulis et al., 2003; Schofield et al.,2013). The Strait of Sicily has strong south easterly currents year-round (Poulain & Zambianchi, 2007), which may have restricted Turtle 21 from entering the western basin sooner. Strong surface currents may limit hatchling dispersal to this region reducing the likelihood of adult foraging areas in the western basin (Hays et al., 2010; Casale & Mariani, 2014).

For SIA to successfully assign individuals to putative foraging grounds isotopically distinct regions must be used, and three were identified in this study, the Adriatic region, the Tunisian Plateau, and the rest of the eastern Mediterranean (Fig. 2, see Appendix S3a). Individuals in the Adriatic region have relatively low $\delta^{13}C$ values and high $\delta^{15}N$ values. This is because they are foraging on food chains strongly influenced by major river systems supplying terrestrial organic matter, which have lower $\delta^{13}C$ values than marine organic matter (Degobbis & Gilmartin, 1990; Vizzini et al., 2005; Zbinden et al., 2011), and are likely to have a substantial amount of highly enriched ^{15}N anthropogenic waste and agricultural run-off (e.g. Degobbis & Gilmartin, 1990; Zbinden et al., 2011). This trend has been previously reported in Mediterranean loggerhead turtles (Zbinden et al., 2011; Cardona et al., 2014), notably, the eastern Mediterranean basin (including the Tunisian Plateau) has high levels of N_2-fixation and therefore lower baseline $\delta^{15}N$ values in comparison to the Adriatic region (Pantoja et al., 2002), explaining the low $\delta^{15}N$ values reported for these foragers.

Individuals foraging on the Tunisian Plateau are foraging further offshore (mean: 68.5 km) than those in the rest of the eastern Mediterranean (mean: 11.0 km) or the Adriatic region (mean: 4.8 km). Although still on the continental shelf it is likely loggerhead turtles on the Tunisian Plateau are foraging on food chains with phytoplankton as the primary producer. Individuals foraging on the Tunisian Plateau have relatively low $\delta^{13}C$ values and high $\delta^{34}S$ values. This is expected as less productive pelagic and oceanic regions supported by phytoplankton have lower $\delta^{13}C$ values and higher $\delta^{34}S$ values in comparison to productive benthic and nearshore regions supported by algae and seagrass (DeNiro & Epstein, 1978; Graham et al., 2010). This trend has been previously reported in benthic communities (Pinnegar & Polunin, 2000) and for green turtles (Cardona et al., 2009; Tucker et al., 2014; Bradshaw et al., 2017).

In total, our study was unable to assign 30% of the Alagadi and 75% of the Zakynthos females sampled to one of three relatively broad geographic regions (Fig. 2, see Appendix S3a). Samples from Zakynthos were run previously for only $\delta^{13}C$ and $\delta^{15}N$ analysis (by Zbinden et al., 2011), which likely contributed to the low assignment success observed. To better understand the spatial variation of loggerhead turtle isotopes in the Mediterranean Sea, we support the recommendation of previous studies (e.g. Ceriani et al., 2012; Seminoff et al., 2012; Bradshaw et al., 2017) in the use of these complementary tracking approaches and urge all future satellite telemetry studies to sample satellite tracked individuals for SIA to understand the spatial ecology of marine vertebrates at a population level. In addition, the collaboration of researchers enabled the data for two major rookeries in the Mediterranean Sea to be combined to better understand the geographical differences in isotope ratios.

This is the first study of this geographical scale in the Mediterranean. A basin-scale collaboration, combining data from foraging and nesting grounds across the Mediterranean, would enable species-specific isoscapes to be created (as recommended by Haywood et al., 2019), which would enhance our understanding on marine turtle ecology in this oceanographically complex region.

To date, only one loggerhead turtle study has analysed δ^{34}S values to assign individuals to foraging grounds (Tucker et al., 2014). The present study is the first study to analyse all three isotopes for loggerhead turtles in the Mediterranean, a method that has been previously reported as vital for distinguishing green turtle foraging grounds in this region (Bradshaw et al., 2017). We strongly support the recommendation by Bradshaw et al. (2017) that sufficient tissue should be sampled to allow analysis of δ^{13}C, δ^{15}N, and δ^{34}S values. The Tunisian Plateau, for example, would not have been distinguishable from the rest of the eastern Mediterranean without δ^{34}S analysis and in turn the importance of this region would not have been highlighted. In addition, if sulphur had been analysed for the Zakynthos nesting population then it is likely a much larger proportion of nesting females would have been assigned to a foraging region. To better delineate isotopic profiles between multiple foraging grounds and help assign more individuals to putative foraging regions, analysis of additional intrinsic markers e.g. trace elements (e.g. Ramirez et al., 2019) or additional analytical techniques such as amino acid compound specific stable isotope analysis (e.g. Seminoff et al., 2012, Vander Zanden et al., 2013) would also be beneficial. This could be especially important in regions of complex geography and oceanography with multiple foraging regions, such as the Mediterranean Sea (Bradshaw et al., 2017).

The large geographical range used by loggerhead turtles in the Mediterranean Sea makes protection challenging and requires a diverse approach to conservation (Wallace et al., 2011). Due to the collaboration of researchers, this is the first SIA study of this geographical scale in the Mediterranean, that combines satellite telemetry and SIA of three isotopes, enabling the critical marine regions of two major loggerhead turtle rookeries to be determined at a population level. This will enable conservation plans to be better informed, targeting foraging grounds that support the largest proportion of major nesting cohorts, where fisheries management can be directed. Continual monitoring of critical marine habitats is vital to detect changes in habitat use resulting from natural or anthropological changes, such as climate change. This would enable successful development of long-term conservation plans. By conducting the longest study of its kind, this research demonstrates the strength of stable isotope tracking to detect shifts in the importance of foraging regions across multiple decades and to direct management and conservation efforts to these critical habitats.

To summarise, to create a more comprehensive picture of where Mediterranean loggerhead turtles are foraging, we combined satellite telemetry and SIA to infer habitat use at a population level. This study confirms the importance of the Tunisian Plateau as a foraging region and as a potential area for future conservation management. We demonstrate high foraging ground fidelity in this population and show that the importance of these foraging regions persists across this multi-decadal study, providing baselines to develop and assess conservation strategies. This work has greatly enhanced our understanding of the movements and habitat use of loggerhead turtles nesting in the regionally important rookery at Alagadi, North Cyprus and demonstrates the advantages of using complimentary tracking techniques to study the spatial ecology of elusive marine vertebrates. This study shows how this method could be a powerful tool in the designation of Marine Protected Areas designed to protect migratory species.

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Biosketch Julia C. Haywood is a marine spatial ecologist with the Marine Turtle Research Group (MTRG) and is interested in where, why, and how animals migrate. This work constitutes part of her PhD at the University of Exeter with ACB, JDS, SW, and WJF. Further information about the MTRG can be found at www.seaturtle.org.uk/mtrg/.

Data availability Statement Data can be made available by contacting the corresponding author directly.

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SUPPORTING INFORMATION

Appendix S1 – Satellite tracking

Raw telemetry data, obtained from the Argos satellite system, were downloaded using the Satellite Tracking and Analysis Tool (Coyne & Godley, 2005) and the Wildlife Computers data portal (wildlifecomputers.com). To ensure a higher accuracy in the location data, filters were applied to the telemetry data using the R-package 'Argosfilter' (Freitas, 2012), removing Z (failed Argos plausibility tests) and 0 (error >1500 m) ARGOS classes (CLS, 2008), and positional data entries with turn angles <15 ° and calculated speeds of >5 km h^{-1} (considered implausible for marine turtles, Witt et al., 2010).

To identify foraging grounds, state-space models were applied to each individual turtle track. Continuous-time correlated random walk models were fitted to de-noise the data using a Kalman-filter in the R-package 'crawl' (function 'crawlWrap', Johnson & London, 2018) and 'momentuHMM' (McClintock & Michelot, 2018). This assumes a bivariate normal measurement error model and outputs a position estimate every 6 hours. It was assumed step length had a gamma distribution and turning angle had a wrapped Cauchy distribution (Langrock et al., 2012). Discrete-time hidden Markov models were then fitted using the R-function 'fitHMM', which estimated the likelihood of the two behavioural states 'transit' (migratory-type movements) and 'resident' (area-restricted-search-type movements, McClintock & Michelot, 2018). Resident behaviour was inferred as foraging and resting, as these behaviours cannot be distinguished from locational data alone (Thums et al., 2017). Locations assigned as resident behaviour were considered foraging grounds if the individual remained for >30 days (Blumenthal et al., 2006). The large spatial distances between potential regions (>2500km) suggests that the uncertainties in the telemetry data will be insignificant.

Table S1.1 Satellite telemetry details of loggerhead turtles tracked from Cyprus (Turtles 1-37) and Greece (Turtles 38-55). CCL: curved carapace length. Data were previously published for Cyprus deployments between 2001 and 2012 (Godley et al., 2003; Broderick et al., 2007; Snape et al., 2016) and Greece deployments (Zbinden et al., 2008, 2011).

Turtle	CCL (m)	δ^{13}C (‰)	δ^{15}N (‰)	δ^{34}S (‰)	Deployment		Manufacturer (Model)	Tracking Duration	Foraging Ground	Nesting Seasons
					Year	Site				
1	0.708	-11.92	5.44	NA	2001	Alagadi	Telonics (ST14)	80	Cyprus	4
2	0.725	NA	NA	NA	2001	Alagadi	Telonics (ST14)	59	Syria	3
3	0.733	-12.03	6.28	17.69	2002	Alagadi	SMRU (SRDL)	422	Tunisia	9
4	0.728	NA	NA	NA	2002	Alagadi	Telonics (ST14)	391	Libya	6
5	0.722	NA	NA	NA	2002	Alagadi	Telonics (ST6)	404	Cyprus	6
6	0.685	-15.71	6.66	NA	2002	Alagadi	SMRU (SRDL)	138	Libya	4
7	0.710	NA	NA	NA	2002	Alagadi	Telonics (ST6)	226	Egypt	2
8	0.689	NA	NA	NA	2002	Alagadi	Telonics (ST14)	86	Egypt	1
1	0.733	-11.92	5.44	NA	2003	Alagadi	Telonics (ST18)	1405	Cyprus	4
9	0.774	-15.2	8.41	NA	2003	Alagadi	Telonics (ST18)	627	Syria	2
4	0.749	NA	NA	NA	2004	Alagadi	Telonics (ST18)	70	NA	6
3	0.733	-12.03	6.28	17.69	2005	Alagadi	Sirtrack (Kiwisat 101)	176	Tunisia	9
10	0.817	-16.88	10.725	22.12	2005	Alagadi	Sirtrack (Kiwisat 101)	6	NA	7
11	0.756	NA	NA	NA	2005	Alagadi	Sirtrack (Kiwisat 101)	137	Egypt	2
12	0.782	-15.23	4.83	18.8	2006	Alagadi	SMRU (SRDL)	63	NA	6
13	0.770	-15.44	11.575	NA	2006	Alagadi	SMRU (SRDL)	351	Tunisia Plateau	2
14	0.650	NA	NA	NA	2006	Alagadi	SMRU (SRDL)	348	Libya	1
15	0.850	-14.75	9.86	NA	2007	Alagadi	SMRU (SRDL)	261	Lebanon	1
16	0.670	-16.59	7.73	NA	2007	Alagadi	SMRU (SRDL)	144	Libya	1
17	0.657	NA	NA	NA	2008	Alagadi	SMRU (SRDL)	700	Cyprus	1
18	0.649	-15.23	10.56	17.02	2009	Alagadi	SMRU (SRDL)	267	Syria	2
19	0.779	-12.09	7.31	17.66	2017	Alagadi	Wildlife Computers (SPOT)	541	Lebanon	7
20	0.806	-15.8	15.29	15.84	2017	Alagadi	Wildlife Computers (SPOT)	102	Italy	3
21	0.679	-16.74	7.64	22.66	2017	Alagadi	Wildlife Computers (SPOT)	466	Oceanic	2
22	0.762	-17.66	9.07	22.24	2017	Alagadi	Wildlife Computers (SPOT)	435	Tunisia Plateau	2
23	0.743	-14.81	11.68	17.9	2017	Alagadi	Wildlife Computers (SPOT)	200	Israel	1
24	0.803	-11.99	9.67	14.3	2018	Alagadi	Wildlife Computers (SPOT)	169	Tunisia	3
25	0.738	-15.98	7.78	14.4	2018	Alagadi	Wildlife Computers (SPOT)	221	Cyprus	4
26	0.677	-17.26	9.24	19.66	2018	Alagadi	Wildlife Computers (SPOT)	521	Tunisia Plateau	2
27	0.653	-17.24	7.94	20.25	2018	Alagadi	Wildlife Computers (SPOT)	222	Oceanic	2
28	0.694	-15.78	9.34	19.39	2018	Alagadi	Wildlife Computers (SPOT)	183	Tunisia Plateau	2
29	0.677	-15.1	10.12	20.58	2018	Alagadi	Wildlife Computers (SPOT)	193	Turkey	2
30	NA	NA	NA	NA	2011	Akdeniz	Sirtrack (K2G)	403	Syria	NA
31	NA	NA	NA	NA	2011	Akdeniz	Sirtrack (K2G)	440	Egypt	NA
32	NA	NA	NA	NA	2012	Iskele	Sirtrack (F4)	174	Libya	NA
33	NA	NA	NA	NA	2012	Iskele	Sirtrack (K2G)	334	Tunisia Plateau	NA
34	NA	NA	NA	NA	2012	Iskele	Sirtrack (K2G)	219	Egypt	NA
35	NA	NA	NA	NA	2012	Iskele	Wildlife Computers (SPOT)	212	Tunisia	NA
36	NA	NA	NA	NA	2012	Iskele	Wildlife Computers (SPOT)	1252	Cyprus	NA
37	NA	NA	NA	NA	2011	Tatlisu	Sirtrack (K2G)	2007	Cyprus	NA
38	0.850	NA	NA	NA	2004	Zakynthos	Sirtrack (Kiwisat 101)	128	Adriatic (north)	2
39	0.860	NA	NA	NA	2004	Zakynthos	Sirtrack (Kiwisat 101)	147	Italy	7
40	0.910	NA	NA	NA	2004	Zakynthos	Sirtrack (Kiwisat 101)	740	Gulf of Tunis	2
41	0.790	NA	NA	NA	2005	Zakynthos	Sirtrack (Kiwisat 101)	189	Adriatic (north)	NA
42	0.987	-16.56	12.39	NA	2005	Zakynthos	Sirtrack (Kiwisat 101)	419	Adriatic (north)	3
43	0.890	NA	NA	NA	2005	Zakynthos	Sirtrack (Kiwisat 101)	392	Adriatic (north)	2
44	0.760	NA	NA	NA	2005	Zakynthos	Sirtrack (Kiwisat 101)	119	Tunisia Plateau	NA
45	0.860	-17.4	10.62	NA	2007	Zakynthos	Telonics (A-2010)	114	Tunisia Plateau	5
46	0.855	-18.67	13.59	NA	2007	Zakynthos	Telonics (A-2010)	325	Amvrakikos	NA
47	0.815	-16.9	9.62	NA	2007	Zakynthos	Telonics (A-2010)	386	Tunisia Plateau	2
48	0.845	-16.9	11.28	NA	2007	Zakynthos	Telonics (A-2010)	220	Croatia (south)	NA
49	0.785	-17.93	9.41	NA	2007	Zakynthos	Telonics (A-2010)	430	Tunisia Plateau	NA
50	0.880	-16.78	10.33	NA	2007	Zakynthos	Telonics (A-2010)	412	Adriatic (north)	4
51	0.870	-17.1	11.47	NA	2007	Zakynthos	Telonics (A-2010)	418	Adriatic (north)	2
52	0.760	-17.67	12.84	NA	2007	Zakynthos	Telonics (A-2010)	204	Amvrakikos	NA
53	0.890	-16.8	8.34	NA	2007	Zakynthos	Sirtrack (Kiwisat 101)	145	Tunisia Plateau	NA
54	0.820	-16.89	7.87	NA	2007	Zakynthos	Sirtrack (Kiwisat 101)	452	Tunisia Plateau	3
55	0.775	-12.78	7.49	NA	2007	Zakynthos	Sirtrack (Kiwisat 101)	673	Tunisia Plateau	NA

Appendix S2 – Stable isotope analysis

Epidermis tissue samples were rinsed with deionized water, soaked for 24 hours, dried at 60 ˚C for 48 hours, and weighed in a sterilised tin capsule prior to analysis. For carbon and nitrogen stable isotope analysis 0.0007 g (+/-0.0001 g) of sample was required and 0.004-0.0055 g was required for sulphur analysis. Vanadium pentoxide (<0.001 g) was added to sulphur samples (Bradshaw et al., 2017). In some cases, it was not possible to process an individual for sulphur due to insufficient sample mass (n=53, including six satellite tracked females). Lipid extraction was not undertaken and samples did not require a lipid correction factor as evaluated by the C:N ratio (mean:3.44, Post et al., 2007).

Stable isotope analysis was conducted (Elemtex Ltd, UK laboratory) with samples being analysed on a Thermoquest EA1110 elemental analyser linked to a Sercon2020 stable isotope ratio mass spectrometer running in continuous flow mode. Isotope ratios are expressed as conventional delta (δ) values in parts per thousand (‰) using the following equation: $\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$, where X is ^{13}C, ^{15}N, or ^{34}S. R_{sample} and $R_{standard}$ are the corresponding ratios of the heavier to the lighter isotope (i.e. $^{13}C/^{12}C$, $^{15}N/^{14}N$, $^{34}S/^{32}S$) in the sample and international standard, respectively. The international standard, for ^{13}C, ^{15}N, and ^{34}S is Vienna Pee Dee Belemnite, atmospheric nitrogen (AIR), and Vienna Cañon Diablo Trolite, respectively.

Inter-sample variation in isotope ratios

Epidermis samples from the left and right fore-flipper of the same individual taken on the same date did not significantly differ in $\delta^{13}C$ or $\delta^{15}N$ values (Wilcoxon matched pairs test, $\delta^{13}C$: V=365, Z=0.20, p=0.84, n=38, $\delta^{15}N$: V=492.5, Z=1.77, p=0.08, n=38). The results were insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S4). This suggests that one sample represents the isotopic ratios of an individual accurately, therefore, if multiple samples were analysed, the mean isotope ratio was used for further analysis. Due to the restricted size of tissue samples, differences were unable to be tested for $\delta^{34}S$ values.

Inter-clutch variation in isotope ratios

This is the first study to determine isotopic shifts in epidermis samples successively collected across a nesting season. Epidermis samples were obtained from the third membrane of the right fore-flipper whilst laying the first clutch and the left fore-flipper whilst laying the second clutch. Both flippers were used to reduce flipper membrane damage, which will not affect the results as no significant difference in isotope values were reported between flippers (see Appendix S2a). The $\delta^{13}C$ and $\delta^{34}S$ values of epidermis samples did not vary significantly across successive clutches of the same female ($\delta^{13}C$: Wilcoxon matched pairs test, V=173, Z=-0.99, p=0.34, n=30, $\delta^{34}S$: Paired t-test, t_{15}=-0.49, p=0.63, n=16) but $\delta^{15}N$ values did vary ($\delta^{15}N$: Paired t-test, t_{15}=-3.54, p=0.001, n=30, Fig S2.1).

The mean difference in $\delta^{15}N$ values was 0.44 ‰ (range = -0.73 to 1.44 ‰), which is not considered biologically relevant as the difference can be either positive or negative (Fig S2.1) and the difference in nitrogen isotope values between clutches was smaller than the difference in isotope values among foraging areas, thus, tissue samples collected from either clutch could be used for foraging ground assignment. However, for the isotope ratios to best represent the foraging ground, we support the recommendation of Haywood et al. (2019), that the isotope ratio of the first encountered clutch should be used for further analysis. The results were insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S4).

Flipper versus shoulder epidermis tissue samples

Regular biopsy sampling and flipper tagging of the same individuals was found to lead to flipper damage, and thus we explored taking tissue samples from the shoulder as a less detrimental, long-term alternative. This is the first study to investigate if shoulder and flipper epidermis samples can be used interchangeably. The $\delta^{13}C$ and $\delta^{15}N$ values in the flipper and shoulder epidermis samples collected from an individual on the same date differed significantly (Wilcoxon matched pairs test, $\delta^{13}C$: V=206, Z=-4.06, p<0.001, n=51, $\delta^{15}N$: V=1064, Z=4.13, p<0.001, n=51) whilst $\delta^{34}S$ values did not (Paired t-test, $\delta^{34}S$: t_{17}=2.15, p=0.05, n=18). These results were insensitive to the isotope analytical uncertainties with the exception of $\delta^{34}S$ values where only 54% of the repeats had p>0.05 and therefore a conversion equation (see below for details on the conversion equation) was also created for flipper and shoulder $\delta^{34}S$ values (for details of the uncertainty analysis see Appendix S4). The mean difference in $\delta^{13}C$ values was -0.27 ‰ ± 0.43 ‰ (range = -1.15 to 1.08 ‰) and $\delta^{15}N$ values was 0.24 ‰ ± 0.35 ‰ (range = -0.53 to 1.17 ‰) and $\delta^{34}S$ values was 0.35 ‰ ± 0.66 ‰ (range = -0.72 to 2.00 ‰) using flipper samples as the reference.

There was a strong positive correlation between flipper and shoulder epidermis isotope ratios (Spearman's rank-correlation coefficient, $\delta^{13}C$: $\rho=0.94$, $p<0.001$, $n=51$, $\delta^{15}N$: $\rho=0.96$, $p<0.001$, $n=51$, $\delta^{34}S$: $\rho=0.96$, $p<0.001$, $n=21$), hence, shoulder samples could be used as a less intrusive alternative to flipper epidermis sampling or where flipper tagging impedes collection at the flipper. Therefore, for further analysis unknown flipper isotope ratios were estimated from known shoulder isotope ratios using the conversion equations derived from linear regressions ($\delta^{13}C$: $F_{1,49}=890$, $p<0.001$, $R^2_{(Adj)}=0.95$, $\delta^{15}N$: $F_{1,49}=1671$, $p<0.001$, $R^2_{(Adj)}=0.97$, $\delta^{34}S$: $F_{1,16}=356.7$, $p<0.001$, $R^2_{(Adj)}=0.95$, Fig S2.2). Both correlation and linear regression results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S4).

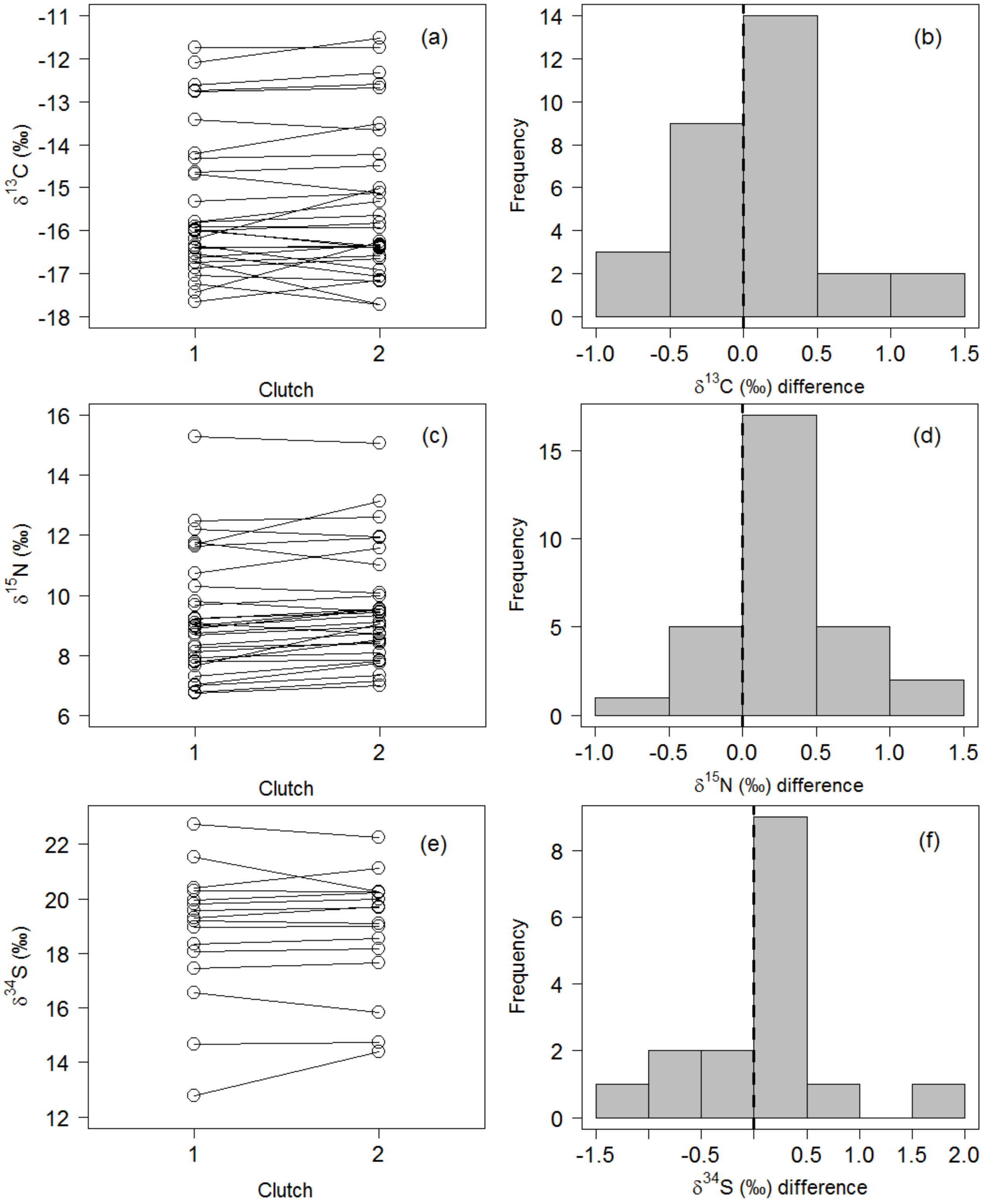

Fig S2.1 (a), (c), and (e) show temporal consistency in $\delta^{13}C$ (n=30), $\delta^{15}N$ (n=30), and $\delta^{34}S$ values (n=16) of samples collected from loggerhead turtles during successive clutches. (b), (d), and (f) show differences in isotope ratios between samples using the first clutch as a reference.

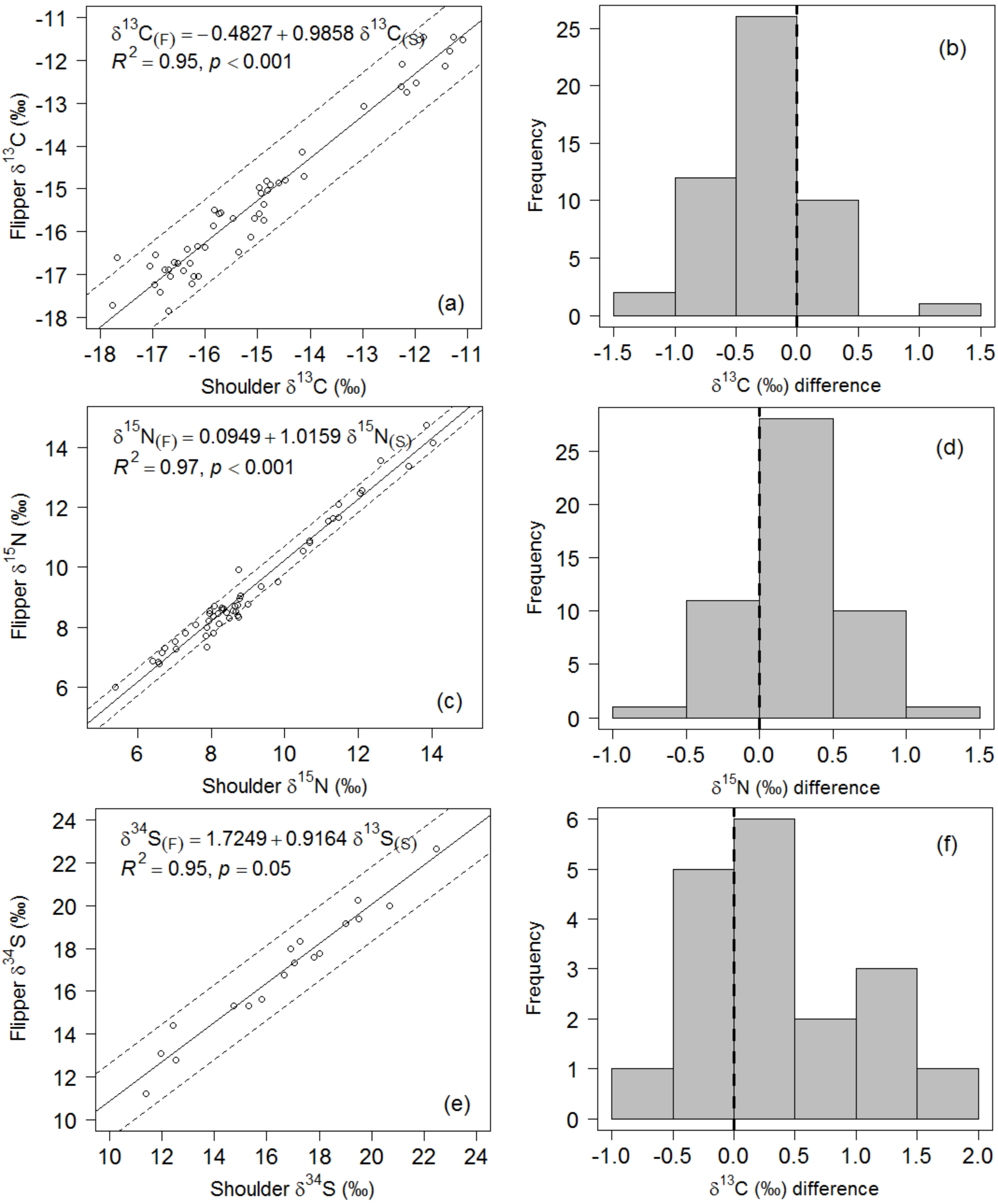

Fig S2.2 (a), (c), and (e) show linear relationships between flipper and shoulder epidermis samples for δ^{13}C (n=51), δ^{15}N (n=51), and δ^{34}S values (n=16) of loggerhead turtles nesting at Alagadi Beach, North Cyprus. Dotted lines depict 95% confidence intervals. Conversion equations and regression statistics are shown. (b), (d), and (f) show differences in isotope ratios between samples using the flipper sample as a reference.

Appendix S3 - Foraging ground assignment

To determine suitable geographical regions which are isotopically distinct i) a Principal Component Analysis was run, ii) data were tested using a Levene's test to show they met the assumption of homogeneity of variances, iii) an Analysis of Variance was used to confirm whether the identified regions were significantly different, and iv) a post hoc Tukey's Honest Significant Difference test performing multiple pairwise comparisons was used to identify which regions differed isotopically. As body size can influence diet (Seney & Musick, 2007) and in turn the isotope ratios of an individual, an Analysis of Covariance was performed to determine if body size differed between foraging regions and a post hoc Tukey's Honest Significant Difference test was used to determine which regions differed. To test whether foraging region continues to affect stable isotope ratios when body size was taken into account, an analysis of covariance was performed.

A MANOVA was also performed and again showed that the overall isotope ratios differed between foraging region (MANOVA, , Pillai's trace test, $F(_{6,20}) = 5.8$, $p = 0.001$), with each isotope differing significantly between the final three foraging regions (ANOVA, $\delta^{13}C$: $F(_{2,11}) = 7.77$, $p = 0.007$; $\delta^{15}N$: $F(_{2,11}) = 6.90$, $p = 0.01$; and $\delta^{34}S$: $F(_{2,7}) = 7.77$, $p = 0.01$).

Identifying isotopically distinct foraging regions

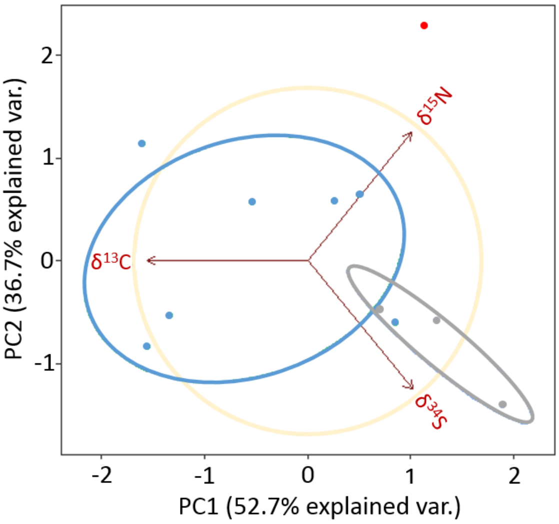

Fig S3.3 Principal Component Analysis results separating loggerhead turtles in to three distinct foraging regions based on $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values: the Adriatic region (red), the Tunisian Plateau (grey), and the rest of the eastern Mediterranean (blue).

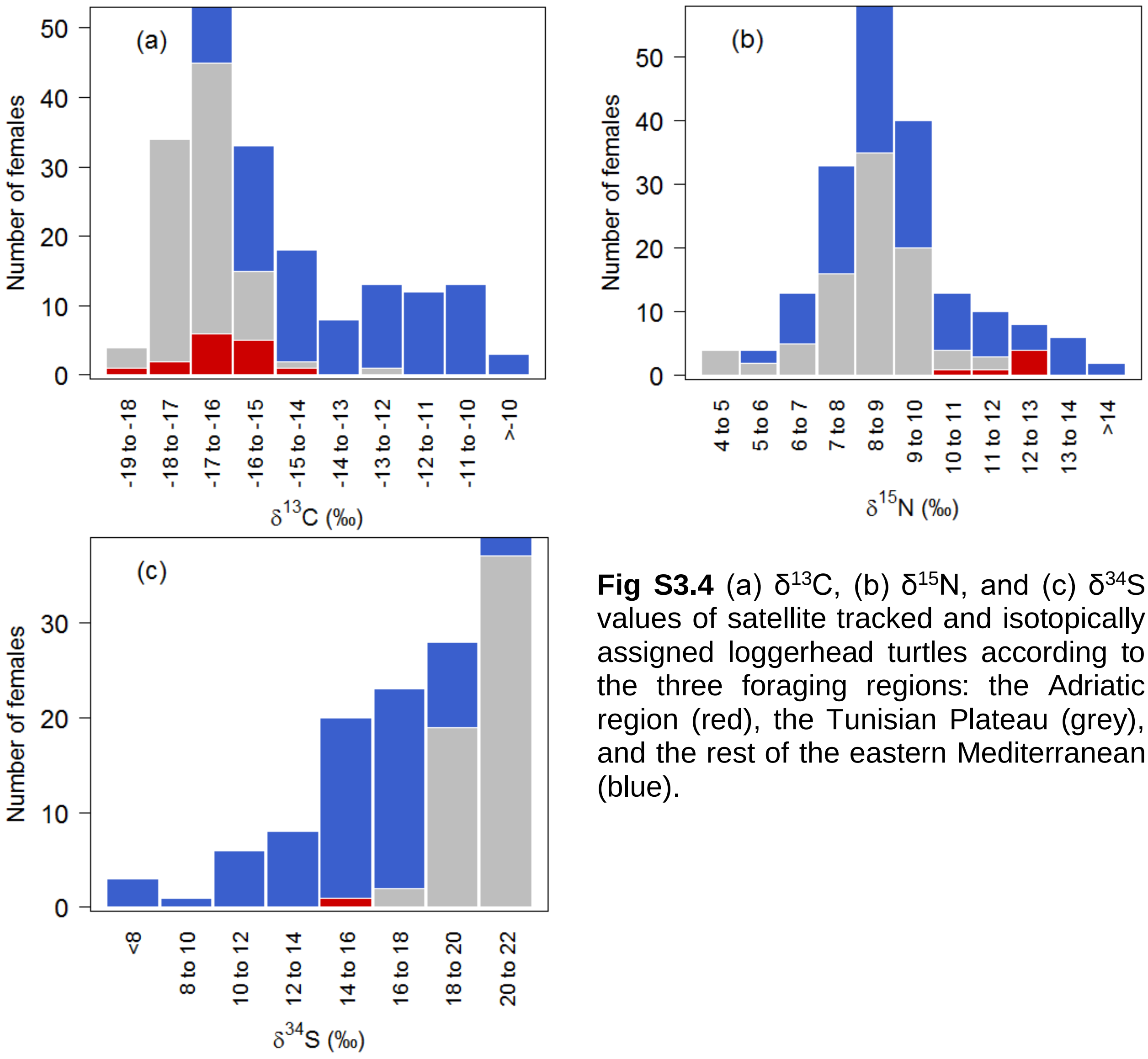

Fig S3.4 (a) $\delta^{13}C$, (b) $\delta^{15}N$, and (c) $\delta^{34}S$ values of satellite tracked and isotopically assigned loggerhead turtles according to the three foraging regions: the Adriatic region (red), the Tunisian Plateau (grey), and the rest of the eastern Mediterranean (blue).

Table S3.2 (a) Post hoc Tukey's Honest Significant Difference results comparing stable isotope ratios of satellite tracked loggerhead turtles among the three foraging regions. Significant p-values ($p < 0.05$) in **bold**. (b) Range and mean (in parenthesis ‰) of isotope ratios of satellite tracked and isotopically assigned loggerhead turtles in the three foraging regions. Only one Adriatic region individual was sampled for δ^{34}S.

Region	δ^{15}N	δ^{34}S	δ^{13}C
(a)			
Adriatic region - East Mediterranean	**<0.001**	0.80	**<0.001**
Adriatic region - Tunisian Plateau	**0.002**	0.16	0.73
Tunisian Plateau - East Mediterranean	0.24	**0.03**	**0.001**
(b)			
Adriatic region	10.33 to 16.60 (13.10)	15.84	-18.67 to -14.89 (-16.48)
Tunisian Plateau	4.44 to 11.58 (8.32)	17.08 to 23.39 (20.61)	-18.96 to -12.78 (-16.78)
East Mediterranean	5.44 to 12.80(8.85)	1.62 to 20.58 (15.32)	-16.59 to -8.18 (-13.33)

Table S3.3 (a) Discriminant Function Analysis assignments of loggerhead turtles to the three foraging regions based on δ^{13}C, δ^{15}N, and δ^{34}S values with posterior probabilities of ≥80%. Adriatic = Adriatic region, Tunisia = Tunisian Plateau, Other = rest of the eastern Mediterranean. Number and percentages (in parenthesis) shown. (b) Percent of satellite tracked females assigned to the correct foraging ground.

(a)			Predicted foraging region			
Dataset	n	Location	Adriatic	Tunisia	Other	Total
Training	31	Adriatic	6 (75)	1 (12.5)	1 (12.5)	8
		Tunisia	1 (8)	9 (69)	3 (23)	13
		Other	0	1 (10)	9 (90)	10
Test	263	Unknown	8 (5)	75 (47)	78 (48)	161
		Total	15 (8)	86 (45)	91 (47)	192
(b)		Sample Population				
LDA		Alagadi	Zakynthos			
δ^{13}C, δ^{15}N		69%	83%			
δ^{13}C, δ^{15}N, δ^{34}S		73%	NA			

Body size Analysis

A significant difference was seen in body size between foraging regions (Analysis of Variance: $F_{2,28}$= 8.36, p=0.001) and a post hoc Tukey's Honest Significant Difference test shows this was due to the females foraging in the Adriatic region being significantly larger than individuals in the rest of the eastern Mediterranean (p=0.001, Fig S5). When body size was taken into account, foraging region continued to affect stable isotope ratios (Analysis of Covariance, δ^{13}C: $F_{2,25}$= 11.99, p<0.001, δ^{15}N: $F_{2,25}$=14.62 , p<0.001, δ^{34}S: $F_{2,7}$= 4.47, p=0.05). However, it must be noted this result is based on very few individuals for the Adriatic region (n=4) and therefore this result should be taken with caution. Both Analysis of Variance and Analysis of Covariance results were found to be insensitive to the isotope analytical uncertainties (for details of this analysis see Appendix S4).

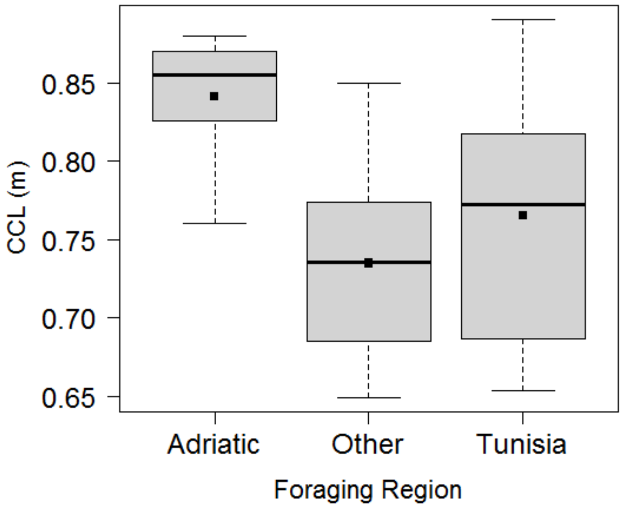

Fig S3.5 Body size of females satellite tracked from Cyprus and Greece foraging in three foraging regions; Adriatic = Adriatic region (n=4), Other = the rest of the eastern Mediterranean (n=77), and Tunisia = Tunisian Plateau (n=90). CCL = curved carapace length. Midline = median, box = interquartile range, whiskers = 5 and 95 percentiles, square = mean.

Appendix S4 – Number of females in the Alagadi nesting cohort assigned to foraging grounds.

Table S4.4 Number of individuals from the Alagadi nesting cohort assigned to the Adriatic region (Adriatic), the Tunisian Plateau (Tunisia), or the rest of the eastern Mediterranean (Other) or remained unassigned (Unassigned) between 1993 and 2018. Total number of individuals sampled is shown.

Year	Adriatic	Tunisia	Other	Unassigned	Total
1992	0	0	1	0	1
1993	0	1	0	0	1
1994	0	0	0	0	0
1995	0	0	1	0	1
1996	0	0	0	1	1
1997	0	3	2	0	5
1998	0	0	0	1	1
1999	0	1	4	0	5
2000	0	2	1	1	4
2001	0	0	2	1	3
2002	0	3	3	0	6
2003	0	1	5	1	7
2004	0	3	1	0	4
2005	0	1	7	5	13
2006	0	3	3	0	6
2007	0	4	9	7	20
2008	0	2	4	0	6
2009	0	7	11	8	26
2010	0	4	5	7	16
2011	0	6	9	1	16
2012	1	6	6	2	15
2013	0	17	13	5	35
2014	1	16	7	6	30
2015	1	7	7	6	21
2016	1	14	13	10	38
2017	2	3	10	6	21
2018	1	7	17	6	31

Appendix S5 – The sensitivity of LDA analysis and foraging ground assignment to the isotope analytical uncertainties

To determine the robustness of our results each statistical analysis underwent uncertainty analysis. This is the first marine turtle study to perform uncertainty analysis on the results of SIA. We recommend all future studies follow this method, so the robustness of each result is understood. Analytical precision for $\delta^{13}C$ and $\delta^{15}N$ values was 0.18‰ and 0.2‰, respectively, determined as the standard deviation from the reference materials $USGS_{40}$, $USGS_{41}$, and BLS, whilst analytical precision for $\delta^{34}S$ values was 0.44 ‰, determined as the standard deviation from the reference materials $USGS_{42}$, $USGS_{43}$, IAEA S1, and IAEA S2. Analytical accuracy was calculated as the sample variance across all samples (see Table S4.2 for values). The combined analytical uncertainty was estimated as a sum of squares of the analytical precision and accuracy assuming that they are uncorrelated (see Table S4.2 for values). Therefore, to identify that the results are insensitive to the combined isotope analytical uncertainties, each analysis was repeated 100 times whilst perturbing the isotope data using additive noise. Noise was calculated as random values following a truncated Gaussian distribution centred on zero with a standard deviation equal to the combined analytical uncertainty. For each analysis the percentage of repeats with a p-value that meets the desired p-value was calculated (see Table S4.2 for values). For foraging ground assignment, propagating the combined analytical uncertainty for both $\delta^{13}C$ and $\delta^{15}N$ values through the LDA classification gave 70±0.1% (median ± standard deviation). The equivalent result for the LDA classification using $\delta^{13}C$, $\delta^{15}N$, and $\delta^{34}S$ values gave 73±0.1% (median ± standard deviation).

Table S5.5 Uncertainty analysis results. % of repeats: percentage of repeats with the desired p-values which are shown in parenthesis.

Statistical analysis	**Isotope ratio**	**Analytical accuracy (‰)**	**Analytical Precision (‰)**	**Combined analytical uncertainty (‰)**	**% of repeats**
Inter-sample variation in isotope ratios					
	Carbon	0.06	0.18	0.19	100 ($p>0.05$)
	Nitrogen	0.07	0.20	0.21	89 ($p>0.05$)
	Sulphur	NA	0.44	NA	NA
Inter-clutch variation in isotope ratios					
	Carbon	0.10	0.18	0.21	100 ($p>0.05$)
	Nitrogen	0.17	0.20	0.26	100 ($p<0.05$)
	Sulphur	0.19	0.44	0.48	100 ($p>0.05$)
Flipper versus shoulder epidermis tissue samples					
T-test	Carbon	0.13	0.18	0.22	100 ($p<0.05$)
	Nitrogen	0.09	0.20	0.22	100 ($p<0.05$)
	Sulphur	0.26	0.44	0.51	54 ($p>0.05$)
Correlation	Carbon	0.13	0.18	0.22	100 ($p<0.05$)
	Nitrogen	0.09	0.20	0.22	100 ($p<0.05$)
	Sulphur	0.26	0.44	0.51	100 ($p<0.05$)
Linear Regression	Carbon	0.13	0.18	0.22	100 ($p<0.05$)
	Nitrogen	0.09	0.20	0.22	100 ($p<0.05$)
	Sulphur	0.26	0.44	0.51	100 ($p<0.05$)
Identifying isotopically distinct foraging regions					
Analysis of Variance	Carbon	2.14	0.18	2.15	100 ($p<0.05$)
	Nitrogen	2.74	0.20	2.75	100 ($p<0.05$)
	Sulphur	2.20	0.44	2.24	80 ($p<0.05$)
Analysis of Covariance	Carbon	2.14	0.18	2.15	100 ($p<0.05$)
	Nitrogen	2.74	0.20	2.75	100 ($p<0.05$)
	Sulphur	2.20	0.44	2.24	94 ($p<0.05$)
Foraging site fidelity					
	Carbon	0.33	0.18	0.37	100 ($p<0.05$)
	Nitrogen	0.25	0.20	0.32	100 ($p<0.05$)
	Sulphur	1.46	0.44	1.52	100 ($p<0.05$)

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CHAPTER 5: MARINE TURTLES ALTER THEIR MIGRATORY BEHAVIOUR IN RESPONSE TO ENVIRONMENTAL CONDITIONS

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Abstract

The environmental conditions that marine turtles experience during migration differ both spatially and temporally, yet how they respond to these changes has received little attention. This study evaluates the influence of environmental conditions on the migratory corridors and dive behaviour of two sympatric Mediterranean turtle species (loggerhead turtles = 37, green turtles = 50). The results show that vertical migratory dive behaviours of these marine turtles are influenced by local, fine-scale, changes in environmental conditions, with individuals diving deeper (4 m to 40 m) for longer (10 to 30 minutes) to avoid high sea states, spending more time in surface waters (2 to 12 minutes) when sea temperature increased, and conducting shallower dives during the night (30 m to 23 m). The species-specific migratory corridors had similar environmental properties (magnetic field intensity, sea temperature, thermal fronts, surface geostrophic and Ekman currents, and wind), suggesting both species may be following similar large-scale environmental cues. However, we suggest migratory routes may be dependent on the physiology of each species, with a trade-off between reducing migratory distance, minimising time from foraging, minimising swimming effort, whilst attempting to remain in favourable conditions by staying within warmer waters. With environmental-driven changes in migration likely in the dynamic ocean, especially as climate change continues, a better understanding of these cues, preferences, and responses are needed to implement effective long-term conservation.

Key words: dynamic ocean management, satellite telemetry, satellite remotely sensed data, dive profiles, Mediterranean, climate change, sea state, diel patterns, migratory corridor

1. Introduction

Migration is the cyclic movement between distant habitats to exploit temporally abundant resources (Robinson et al., 2009). The phenomenon of migration is taxonomically widespread and a vital component to the life history of many species (Webster 2002). In many cases, migrations cover vast distances with individuals travelling through numerous habitats resulting in exposure to varying environmental conditions. Understanding the distribution, migratory connectivity, and environmental influences on migratory species can be challenging, but this information is critical for identifying threats faced by climate change and more immediate anthropogenic pressures (Dunn et al., 2019).

Due to their reliance on multiple dynamic and seasonal habitats, migratory species are considered particularly vulnerable to climate change (Robinson et al., 2009). To effectively protect marine migrants, we need to not only know their distribution but also how they interact with, and are influenced by, the dynamic marine environment (Luschi et al., 2003a; Jeffers & Godley 2016). Shifts in ocean climate could cause environmentally driven changes in migration, but the likely impact of this is unknown. Previous work investigating the influence of long-term environmental changes on marine migrants has shown shifts in migrations due to changes in habitat suitability (Block et al., 2011 and references therein). For example, changes in prey abundance and location of foraging grounds may result in longer migrations (e.g. Keiper et al. 2005; Perry et al., 2005), changes in sea temperature may cause shifts in migratory routes and migratory distances due to thermal tolerances (McMahon & Hays, 2006), whilst shifts in the magnitude and direction of ocean currents might influence migratory routes (e.g. Huse & Ellingsen, 2008). Climate change may affect the cues used to initiate the onset of migrations, resulting in a mismatch in predator presence and optimum resource availability (e.g. Beaugrand et al., 2003; Edwards & Richardson, 2004). In addition, climate driven locational shifts in human activities could increase their detrimental interactions with migrating species (e.g. Southall et al., 2006).

The response of an individual to climate change, will likely depend on their behavioural plasticity (Pulido & Berthold, 2003). Those able to modify behaviours will be more likely to respond sufficiently and survive (Pulido & Berthold, 2003; Robinson et al., 2009). It has recently been highlighted that the response of marine species to local, short-term changes (instead of large, long-term changes), in environmental conditions will better represent their behaviour under future climate scenarios (Bates et al., 2018). This focus on short-term environmental changes will enable responses to be documented on spatial and temporal scales which are more relevant at an individual level (Bates et al., 2018). However, few studies have investigated short-term changes in migratory behaviours even though changes in wind (Kavanagh et al., 2017), waves (Storch et al., 2006), and sea temperature (e.g. McIntyre et al., 2011), are known to affect distributions and dive behaviours of marine species. Greenhouse gas emissions from human activities has resulted in a dramatic rise in global temperatures (IPCC, 2019). Future climate scenarios show sea temperatures, and extreme weather events, resulting in higher wind speeds and wave heights, will increase due to the absorption of excess heat by the oceans and shifts in large scale weather systems (IPCC, 2019). Therefore, understanding the influence of these oceanographic factors on the movements of migrants is important.

Satellite telemetry is regularly used to investigate migrant movements and is a valuable tool for highlighting high-use areas, such as migratory corridors, to inform conservation management (e.g. Block et al., 2011) and the development of transmitters recording dive data has enabled 3-dimensional habitat use to be documented (Hochscheid, 2014; Hussey et al., 2015). Satellite observations and model re-analysis data provide environmental information for observing or indicating conditions within highly dynamic ocean systems, enabling analysis across a range of spatial and temporal scales. Analysing these data in conjunction with vertical and horizontal movements of marine migrants from satellite telemetry data will allow us to better understand the phenomenon of migration within the dynamic ocean, towards better understanding how migrants respond to changes in environmental conditions, which in turn will enable more effective long-term conservation plans.

Marine turtles make migrations over thousands of kilometres between specific nesting and foraging grounds (e.g., Shillinger et al., 2008). Limited research has investigated the influence of oceanographic conditions on marine turtle behaviour, particularly during migrations (Hochscheid, 2014). Most marine turtle research to date, has investigated horizontal movements and their relationship with primary productivity (e.g. Polovina et al., 2004), temperature or thermal fronts (e.g. Hays et al., 2001b; Luschi et al., 2003b; Polovina et al., 2004; Seminoff et al. 2008), and large scale (geostrophic) ocean currents (e.g. Luschi et al., 2003b; Cuevas et al., 2008), rather than the more complete combination of geostrophic and wind driven Ekman currents. Few studies have investigated how vertical migratory dive behaviours are affected by environmental conditions (Hochscheid, 2014). To date, only two studies have investigated how storm conditions affect dive behaviours, with surface avoidance behaviours conducted during storms (Sakamoto et al., 1990; Storch et al., 2006). The influence of temperature on dive behaviour has been investigated for turtles foraging, but not during migrations, and shows the dive response to temperature differs with species and region (e.g. McMahon & Hays, 2006; Weir, 2007; Howell et al., 2010). By analysing satellite telemetry in conjunction with environmental data, this study aims to determine if Mediterranean loggerhead (*Caretta caretta*) and green turtles (*Chelonia mydas*) alter their migratory routes and migratory dive behaviour in response to changes in environmental conditions, including sea state and temperature.

2. Methods

2.1 Satellite telemetry and dive data

Between 1998 and 2019, 87 Platform Terminal Transmitters (PTTs) were attached to adult female loggerhead (n = 37) and green turtles (n = 50) nesting in North Cyprus. Loggerhead turtle PTTs were deployed from four nesting beaches, whilst green turtle deployments were from eight nesting beaches (Fig S1.1). The migratory tracks in this study from 1998 to 2015 were previously published (Godley et al., 2002; 2003; Broderick et al., 2007; Stokes et al., 2015; Snape et al., 2016; Haywood et al., 2020), while nineteen green turtle PTTs (fourteen = Sirtrack FastGPS, five = SPOT Wildlife Computers) were deployed in 2018 and 2019 and are previously unpublished. All tracks, including those previously published, were re-analysed for this study.

Telemetry data, obtained from the Argos satellite system and GPS, were downloaded using the Wildlife Computers data portal (wildlifecomputers.com) and the Satellite Tracking and Analysis Tool (Coyne & Godley, 2005). Filters were applied to the telemetry data to ensure higher accuracy using the R-package ‘Argosfilter’ (Freitas, 2012). This removed positional data entries with turn angles <15 ° and calculated speeds of >5 km h^{-1} (considered implausible for marine turtles, Witt et al., 2010), as well as Z (failed Argos plausibility tests) and 0 (error >1500 m) ARGOS classes (CLS, 2008). GPS data were considered high accuracy and were assigned ARGOS class 3 location quality.

State-space models were applied to each individual turtle track to separate migrations from foraging grounds. To de-noise the data, continuous-time correlated random walk models were fitted using a Kalman-filter in the R-package ‘crawl’ (function ‘crawlWrap’, Johnson & London, 2018) and ‘momentuHMM’ (McClintock & Michelot, 2018). This assumes a bivariate normal measurement error model and outputs a position estimate for every 6 hours. It was assumed turning angle had a wrapped Cauchy distribution and step length had a gamma distribution (Langrock et al., 2012). Using the R-function ‘fitHMM’, discrete-time hidden Markov models were then fitted estimating the likelihood of the two behavioural states ‘transit’ (migratory-type movements) and ‘residential’ (area-restricted-search-type movements, McClintock & Michelot, 2018). Residential behaviours were inferred as both foraging and resting, as from locational data alone these behaviours cannot be distinguished (Thums et al., 2017).

In addition to providing location data, ten PTTs deployed on nine loggerhead and one green turtle which were Sea Mammal Research Unit – Satellite Relay Data Loggers (SMRU SRDLs), also had associated dive data providing information on individual dives and dive profiles. To enhance the locational accuracy of the dive data, each dive was matched with the temporally closest location point from the state-space model output. SMRU SRDLs measured dive duration, surface duration, and maximum dive depth for all recorded dives. Dive profiles were categorised as Profile-A, Profile-C, Profile-E, and Profile-F, based on Hochscheid (2014) categorisations. See S1 in Supporting Information for details of these dive profiles.

2.2 Environmental data

2.2.1 Comparison with migratory corridors

The influence of large-scale environmental conditions on marine turtle migratory corridors were investigated. Options for environmental data include satellite remote sensing, in situ collated datasets or model re-analyses. Satellite observations of temperature and primary productivity would likely provide spatially complete fields but would only be valid for the surface waters. Whereas in situ based datasets, such as International Comprehensive Ocean-Atmosphere Data Set (ICOADS), can provide depth resolved measurements but offer poor spatial coverage and resolution. Therefore, to maximise the potential for coincident matchups between the environmental data and turtle tracking data, spatially complete and fully depth resolved model re-analysis data were used. These re-analysis datasets are free running model analyses, that include assimilation of in-situ observations, and their accuracy has been assessed for the Mediterranean region.

The environmental data compiled included; magnetic field intensity from the CHAOS-6 field model, derived from data collected by Swarm and earlier satellites (including Oersted and CHAMP) as well as from ground observations (Finlay et al., 2016), providing data at six month intervals at a 0.5 degree resolution. Bathymetry data at a 0.063 degree resolution from European Marine Observation and Data Network (EMODnet Bathymetry Consortium, 2018, https://doi.org/10.12770/18ff0d48-b203-4a65-94a9-5fd8b0ec35f6). Monthly sea surface temperature from The Mediterranean Forecasting System (Simoncelli et al., 2019), supplied by the Nucleous for European Modelling of the Ocean (NEMO), provided monthly data at 6 km resolution, and was available from the Mediterranean Sea Physics Reanalysis product (http://marine.copernicus.eu). Monthly thermal ocean front data derived from the Multi-scale Ultra-high Resolution (MUR) temperature dataset, which provided daily data from 2002 - present at 1 km resolution (Miller, 2009), were available from NERC Earth Observation Data Acquisition and Analysis Service (NEODAAS, https://www.neodaas.ac.uk/). Monthly geostrophic and Ekman surface currents from the GLORYS12V1 reanalysis (Rio et al., 2014) provided monthly data at 8 km resolution, and was available from the Global Ocean Physics Reanalysis (http://marine.copernicus.eu). Finally, monthly wind speed from the European Centre for Medium-Range Weather Forecast reanalysis, which provided data at 0.25 degree resolution, and was available from ERA5 (Copernicus Climate Change Service (C3S, 2017), accessed form https://cds.climate.copernicus.eu).

2.2.2 Comparison with migratory dives

Migratory dive behaviours were compared to environmental conditions. Monthly data on primary production and chlorophyll-a concentrations (available from the Mediterranean biogeochemical MedBFM model, which includes data assimilation of surface chlorophyll concentration (Teruzzi et al., 2019)), were downloaded at a 6 km resolution from the Copernicus Mediterranean Sea Biogeochemistry Reanalysis. Monthly sea temperatures were available from the Copernicus Mediterranean Sea Physics Reanalysis. Daily wind speeds from the European Centre for Medium-Range Weather Forecast reanalysis, were downloaded at 0.25 degree resolution from ERA5 (C3S, 2017, https://cds.climate.copernicus.eu). Daily sea surface significant wave height from the global ocean reanalysis wave system of Météo-France (WAVERYS) based on the Meteo France WAve Model (MFWAM), was downloaded at 0.20 degree resolution from Global Ocean Waves Reanalysis (http://marine.copernicus.eu). Finally, mixed layer depth from the GLORYS12V1 reanalysis, was downloaded at 8 km resolution from the Global Ocean Physics Reanalysis (http://marine.copernicus.eu).

Data were available for primary production, chlorophyll-a concentration, and sea temperature for twenty-five depths between 1 and 193 m. Each dive was matched with the temporally closest state-space model output, enabling the dive location to be corrected and the environmental variables were extracted from this location and for all depths when available. To determine what may influence dive behaviour of loggerhead turtles, the effect of location (open sea versus coastal waters), time of day (day versus night), wind speed, significant wave height, and sea surface temperature on dive duration, surface duration, and maximum dive depth were statistically analysed. Each dive was assigned as a day or night dive categorised by local sunrise and sunset times (using the R-package ‘suncalc’, Thieurmel, 2019). A Generalised Additive Mixed Model (GAMM) was then used with significant wave height and sea surface temperature set as smooth terms, location and time of day as factors, and PTT set as the random term. Due to the estimated concurvity exceeding 0.3 between wind speed and sea surface temperature (concurvity = 0.50), wind was not included in the analysis.

All analyses were performed with the software R 3.5.1 (R Core Team, 2018) and for statistical tests, the significance level was alpha = 0.05.

3. Results

3.1 Migratory corridors

Loggerhead turtle PTTs provided locational data for 6 to 2007 days (mean: 364 days, n=37), whilst green turtle PTTs provided data for 26 to 751 days (mean: 226 days, n=50). All migrations from Cyprus started between 8th June and 12th August. Of the eighty-seven PTTs deployed, seventy-nine provided data throughout the post-nesting migrations (hereon migrations) to distinct foraging grounds located on the continental shelf (Fig S2.2 in Supporting Information, loggerhead turtles = 33, green turtles = 46). Loggerhead turtle migrations lasted between 1 and 93 days (mean: 37 days), traveling to nearby foraging grounds in Cyprus or covering up to 3406 km to foraging grounds on the Tunisian Plateau (mean ± SD: 1961 ± 1131 km). Green turtle migrations lasted between 5 and 87 days (mean: 24 days) covering up to 2990 km to reach foraging grounds as far as Tunisia (mean ± SD: 1410 ± 785 km). In addition, two loggerhead turtles conducted oceanic foraging (Fig S2.2 in Supporting Information). Instead of migrating directly to foraging grounds, as would be expected to reduce energetic costs, coastal waters were used *en route* by both species which extended the migratory distance. For further details on individual migratory routes see S2 in Supporting Information.

Species-specific high-use migratory corridors were identified (Fig 1). For loggerhead turtles the major open sea migratory corridor extended from west Cyprus to the Egypt-Libya border (used by 38% of loggerhead turtles), whilst two corridors were evident for green turtles, one from west Cyprus to Egypt and one from east Cyprus to Lebanon (used by 40% and 44% of turtles, respectively, Fig 2). High-use migratory corridors were evident on the coast of Libya for loggerhead turtles, whilst Lebanon, Israel, Egypt, and Libya coasts were heavily used by green turtles (Fig 1). During migrations, loggerhead turtles spent less time in coastal waters compared to green turtles (43% and 64% of their migrations, respectively). For both species, longer migrations resulted in a larger proportion of time in coastal waters, although this was only significant for green turtles (GLM, loggerhead: $F_{(1,22)}$=3.53, p=0.07; green: $F_{(1,41)}$=6.78, p=0.01).

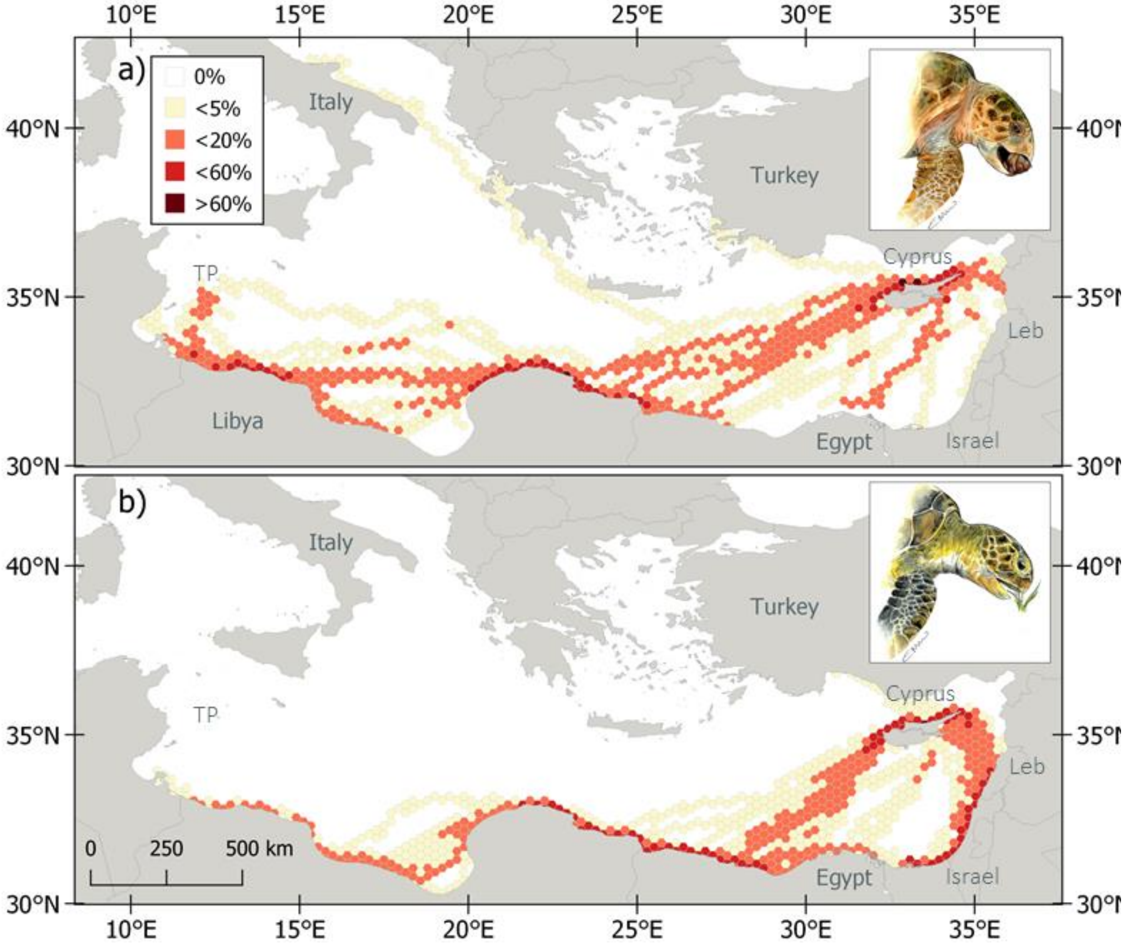

Figure 1 Migratory corridor density map of a) loggerhead (n=33) and b) green turtles (n=46) satellite tracked from Cyprus to foraging grounds. Hexagonal grid cells (0.25° by 0.25°) are coloured by the percentage of turtles using each grid cell. Leb = Lebanon, TP = Tunisian Plateau. Artwork inset of a foraging loggerhead and green turtle.

The migratory corridors of both species were compared to large-scale environmental variables to determine the conditions that were experienced and what possible large-scale environmental cues they may use for navigation (Fig 2). Turtles did not follow ocean fronts during their migration (Fig 2a). However, the apparent targeting of coastal transits rather than travelling directly to foraging grounds, meant both species migrated through warmer waters. Turtles migrating from west Cyprus to north Africa moved from higher to lower sea surface temperatures, with each species exposed to different temperature ranges (Fig 2b). Due to the more westerly location, the loggerhead turtle corridor to north Africa crossed colder waters (22.6 to 24.7 °C) than the green turtle corridor to north Africa (23.5 to 24.7 °C). In comparison, green turtles crossing to Lebanon moved to higher temperatures (24.7 to 25.7 °C). During the initial open sea migrations from Cyprus, both loggerhead and green turtles moved from higher to lower magnetic field intensities (Fig 2c). Magnetic intensity in Cyprus was 46 µT, whilst on the north African and Lebanon coast it was 44 µT and 45 µT, respectively. With different migratory corridors used, each species crossed multiple recirculating ocean surface currents in open seas, whilst there is evidence that both species at some point travelled against ocean surface currents in coastal waters (Fig 2d). In the open seas both species travelled perpendicular to the direction of the wind, whilst in coastal waters they were subject to varying wind directions (Fig 2e). During the open sea migration, landmarks and bathymetric features were not available Fig 2f). In general, the species-specific migratory corridors had similar environmental properties, suggesting both species may be following similar large-scale environmental cues.

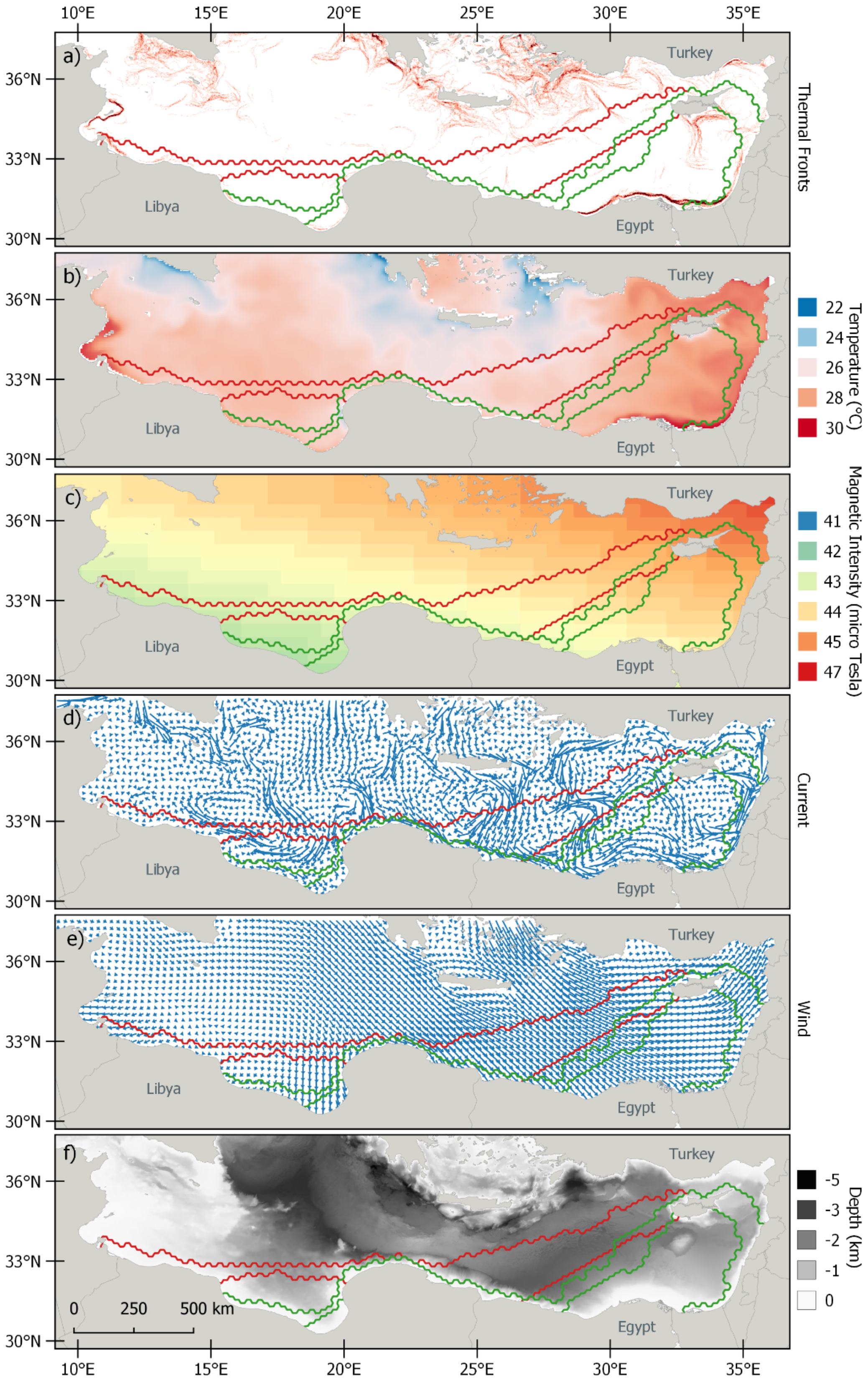

Figure 2 Major migratory corridors of loggerhead (red area) and green turtles (green area) satellite tracked from Cyprus. Environmental variables across the migratory corridors are shown for a) thermal fronts (composite of front direction and persistence), b) sea surface temperature, c) Magnetic field intensity, d) ocean surface currents (Ekman and geostrophic), e) wind, and f) bathymetric depth. Length and direction of arrows in d) and e) represent magnitude and direction, respectively.

3.2 Migratory dives

From the ten SMRU SRDLs, 1475 migratory dives were recorded from nine loggerhead turtles and 50 migratory dives for the green turtle. Dive profiles were available for 16% of dives (± 4, range: 10 to 24%, loggerhead turtle: 9, green turtle = 1), with 336 migratory dive profiles for the loggerhead turtles and unfortunately, only ten migratory dives for the green turtle. For loggerhead turtles, four main dive profiles were evident throughout the migration (Profile-A, Profile-C, Profile-E, and Profile-F; Fig 3). See S1 in Supporting Information for details of these dive types. The proportion of each dive profile differed between open seas and coastal waters, with shallow (<5 m) and Profile-F dives more common in open seas than coastal waters, whilst Profile-A dives were more common in coastal waters than open seas (Fig 3b). During open sea migrations dive duration was shorter (GAMM: t=-1.98, p=0.04) and surface duration was longer (t=8.68, p<0.001) than when in coastal waters, whilst no difference was seen in maximum dive depth (t=-1.37, p=0.17). For further details of this comparison see S3 in the Supporting Information. The one green turtle with a SMRU SRDL followed the same trend with shorter dive duration (although not significant, GLM, F=1.84, p=0.18) and longer surface duration (F=124.80, p<0.001) in the open sea in comparison to coastal waters and conducted deeper dives (F=13.61, p<0.001) in open seas with shallow coastal dives conducted to the seafloor.

Minimum swim speed of both species differed between open seas and coastal waters. Both loggerhead (Generalised Linear Mixed Model with PTT set as the random term; t=6.32, p<0.001, n=22) and green turtles (t=12.39, p<0.001, n=43) swam significantly faster in open seas (Table S3.1). In addition, individuals of both species conducted foraging area restricted search movements in coastal waters whilst one loggerhead likely foraged in open seas (see S2 in Supporting Information). Slower swim speeds and the occurrence of Profile-A dives in coastal waters suggests coastal foraging. For further evidence of foraging *en route* see S3.1 in Supporting Information.

Diel diving patterns were evident for loggerhead turtles, with shallow dives (<5 m) more common during the night than the day (19 and 12% of dives, respectively; Fig 3c). Of the deeper dives (>5 m), during the night the most common dives were Profile-E (44%) and Profile-F dives (23%), whilst a small percent were Profile-C (12%) and Profile-A (10%; Other = 11%). During the day the most common dives were Profile-E (35%), Profile-C (27%), and Profile-A (17%), whilst a small percent were Profile-F dives (10%; Other = 11%). In addition to changes in dive profile, night dives were longer (GAMM; t=2.84, p<0.01) and shallower (t=-6.71, p<0.001) than during the day, whilst no difference was seen in surface duration (t=0.21, p=0.83). The green turtle dived for longer at night (Generalised Linear Model, F=10.71, p<0.01), whilst surface duration (F=0.98, p=0.33) and maximum dive depth did not differ (F=0.11, p=0.74).

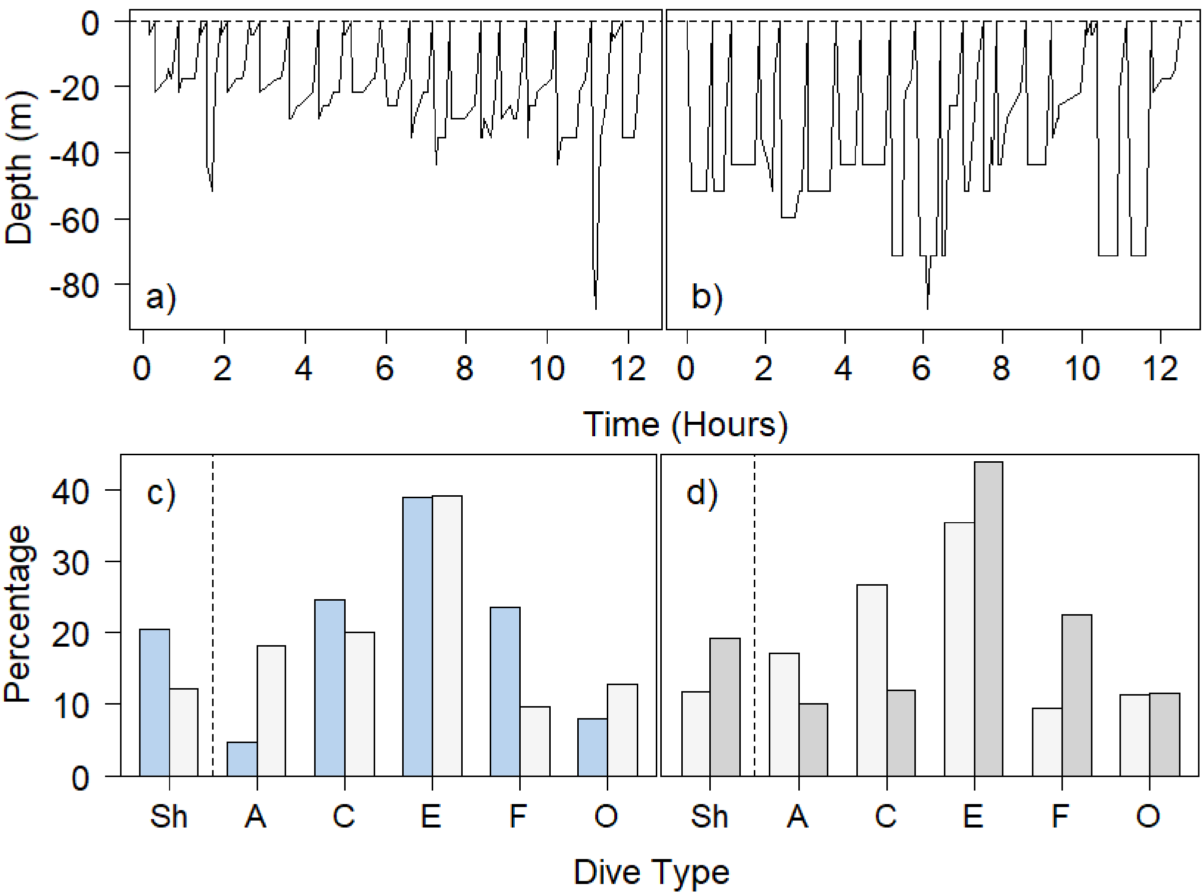

Figure 3 Example dive profiles of a female loggerhead turtle conducting a post-nesting migration in a) open seas (waters >200 m in depth) and b) coastal waters (waters <200 m in depth). Mean percentage of each dive profile categorised as c) open seas (blue) and coastal waters (grey), and d) day (white) and night (grey). Calculated from eight loggerhead turtles with dive data. Sh represents percentage of all dives <5 m in depth. Percentage of dives > 5 m that were Profile A-F, or Other (O).

In both open seas and coastal waters, average maximum dive depth for loggerhead turtles was 26 and 33 m, respectively, with only 20 and 12% of dives less than 5 m in depth. Changes in environmental conditions altered the migratory dive behaviours of migrating turtles. Sea state affected dive behaviours with increased waves resulting in surface avoidance. As significant wave height increased, dives became longer (10 to 30 minutes, GAMM; $F=7.33$, $p<0.001$), deeper (4 to 40 m, $F=2.94$, $p=0.02$), and less time was spent at the surface (6 to 4 minutes, $F=5.86$, $p<0.001$). As sea surface temperature increased, dives became longer (10 to 21 minutes, GAMM; $F=12.23$, $p<0.001$), longer periods were spent at the surface (2 to 12 minutes, $F=3.11$, $p=0.02$), and dives became shallower (20 to 5 m, $F=26.01$, $p<0.001$).

Dives were also visually compared to several environmental conditions. Mixed layer depth occurred between 7.6 and 31.9 m in depth (13.4 ± 2.8 m, Fig 4a). Deep chlorophyll maximum occurred in depths between 90 and 130 m (Fig S6.7 in Supporting Information). Sea temperature decreased with water depth with migratory dives remaining in waters between 15.0 and 28.8 °C (Fig 4b). Primary productivity decreased with depth with dives occurring between 9×10^{-11} and 5×10^{-8} mol m^{-3} (Fig 4c). Neither maximum dive depth nor the gradual ascent phase of Profile-E dives, aligns with mixed layer depth, chlorophyll-a concentration, sea temperature, or primary production (Fig 4).

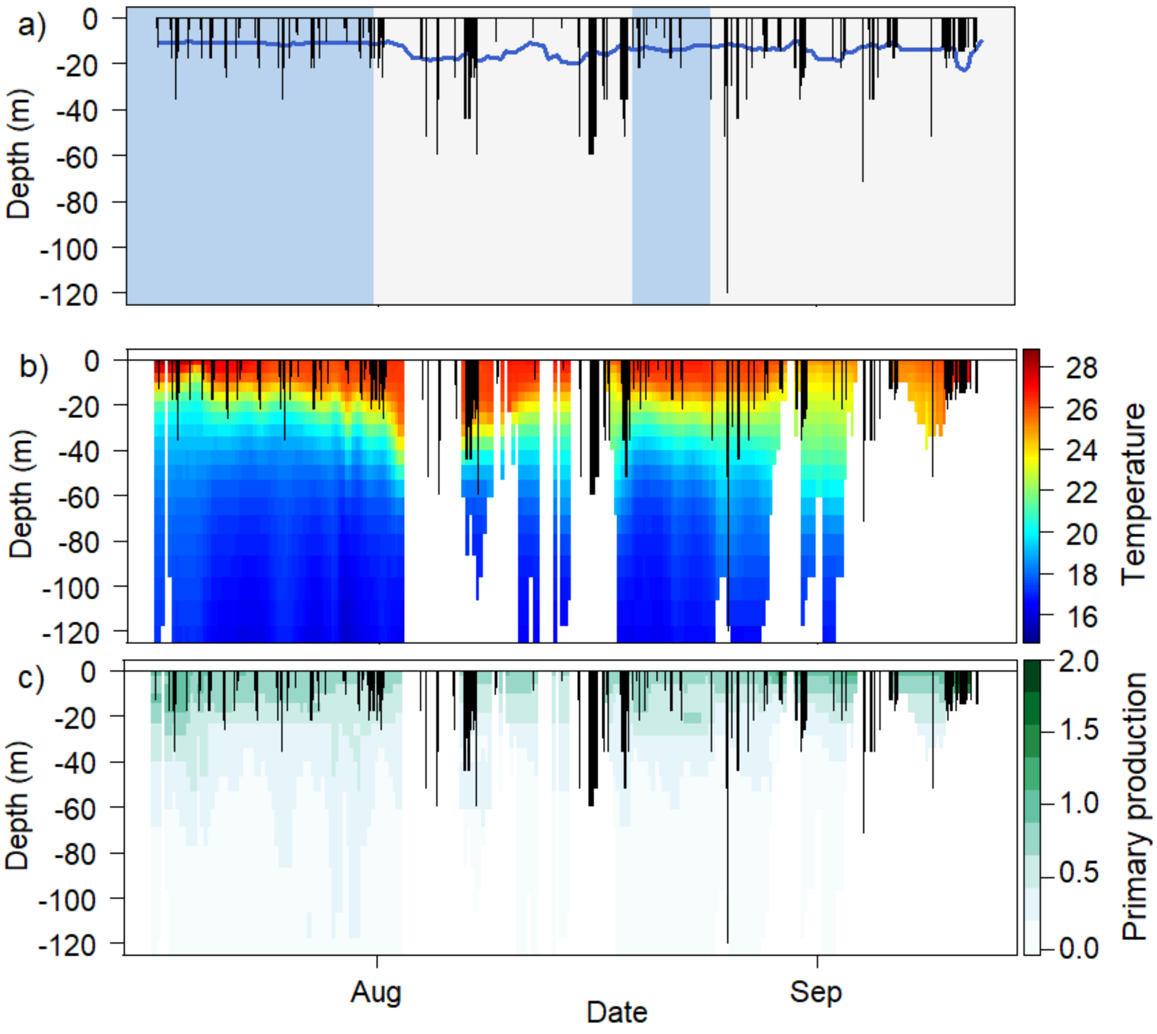

Figure 4 Migratory dives of Turtle_4206 travelling from Cyprus to Tunisia overlaid with a) Mixed layer depth (blue line) as well as the open sea (blue area, >200 m in depth) and coastal water (grey area, <200 m in depth) sections of migration indicated, b) Sea temperature (°C), and c) Primary productivity (1x10^{-8} mol m^{-3}). White sections in b) and c) are locations or depths without sea temperature or primary productivity, respectively.

4. Discussion

This research demonstrates that local fine-scale changes in environmental conditions alter the migratory dive behaviour of marine migrants. This study identifies the plasticity in the vertical dive behaviours of marine turtles in response to location, sea state, temperature, and time of day. Our results suggest migratory routes are likely selected based on the physiology and foraging strategy of each species, and as a compromise between minimising energy expenditure whilst attempting to remain within favourable conditions. Despite species-specific migratory corridors, similar environmental conditions were experienced, including thermal fronts, currents, and magnetic fields, suggesting both species may be following similar large-scale environmental cues.

4.1 Migratory corridors

Identifying key marine regions is a fundamental step for informing effective conservation of marine species. The species-specific foraging grounds and migratory corridors identified in this study support those previously documented for Mediterranean marine turtles (e.g. Casale et al., 2018 and references therein) and highlights the importance of coastal waters as well as open sea corridors.

Previous studies show marine turtle migratory routes are not related to or affected by large scale (geostrophic) ocean currents (Cuevas et al., 2008). This study not only investigated the influence of large-scale surface currents but also wind driven (Ekman) surface currents, which showed both loggerhead and green turtles followed relatively straight-line migratory routes within their species-specific migratory corridors regardless of surface currents. Future studies should include both geostrophic and Ekman currents when investigating the influence of surface currents on migrations towards a better representation of the true oceanographic conditions experienced. Shifts in the ocean current regimes are likely with future climate scenarios (Hoegh-Guldberg & Bruno, 2010). This could displace marine migrants or affect navigation to final destinations. Juvenile marine turtles can return to specific coastal foraging grounds (e.g. Snape et al., 2020) and oceanic foraging adult turtles can return to natal beaches after many years of passive wanderings (Hatase et al., 2002). Therefore, it is likely turtles can compensate for ocean current drift (Luschi et al., 2003b; Hays et al., 2020), which has also been suggested for marine mammals (Horton et al., 2011). Although changes in the magnitude and direction of ocean surface currents may increase the energetic demands of migration, this study shows marine turtles often travel against surface currents and it has been previously documented that adult marine turtles (e.g. Bentivegna et al., 2007; Cuevas et al., 2008) and other taxa (e.g. Horton et al., 2011) can travel against currents with little effect on their swimming abilities and migrations. However, travelling with surface currents would minimise energetic costs (e.g. Horrocks et al., 2001; Luschi et al., 2003a) and exploiting currents has been shown to result in more efficient migrations in other taxa (e.g. fish, Healey et al., 2000; marine mammals, Ream et al., 2005).

Thermal fronts can increase primary productivity and are considered potential prey aggregation zones for many species (Palacios et al., 2006), for example, basking sharks (Sims et al., 1998), tuna (Polovina et al., 2001), and penguins (e.g. Hull et al., 1997). Oceanic foraging has been associated with ocean fronts for marine turtles such as loggerhead, green, and leatherback turtles (e.g. Luschi et al., 2003b; Polovina et al., 2004; Seminoff et al. 2008), whilst no association is seen for post-nesting migrations direct to foraging grounds (e.g. Hays et al., 2001b), which was also the case for the migrants in this study. Although turtles are restricted by lower sea temperatures (Spotila et al., 2017), water temperatures throughout the Mediterranean during the summer months, when post-nesting migrations occur, are well within thermal tolerances. For example, a large proportion of loggerhead turtles nesting in Zakynthos (the largest rookery in the Mediterranean) migrate north to the highest Mediterranean latitudes (Schofield et al., 2013), suggesting migratory routes are not restricted by temperature in the Mediterranean. Despite this, by targeting the coast rather than travelling directly to foraging grounds, the turtles in this study remained on the warm side of thermal fronts. Migratory routes may, therefore, be a compromise between minimising energy expenditure by reducing migration distance as well as remaining in favourable thermal conditions. Thermal fronts have been reported to shift interannually, which could have implications for the distribution and survival of migrating species (Bograd et al., 2004), and shifts in sea temperature, which are expected to continue to change under future climates (IPCC, 2019), have already resulted in range shifts in marine turtles (e.g. McMahon & Hays, 2006) and migrating fishes (e.g. Perry et al., 2005).

It would be expected for these sympatric species to be resilient to similar environmental ranges, and therefore, with different migratory corridors used but similar environmental conditions experienced, it raises the question of what causes these species-specific corridors. It is likely other factors are also influencing migratory routes, such as their physiology, foraging strategy and resources, differing ability or preference for sustained travel, and the location of the final destination. Green turtles undertook a more direct route to the coast where they can forage on seagrass and algae (Bjorndal 1997; Cardona et al., 2010), whilst loggerhead turtles could forage in open seas on gelatinous plankton (jellyfish and tunicates) as well as foraging in coastal waters on invertebrates (molluscs and crustaceans) and fish (Bjorndal 1997; Tomás et al., 2001; Lazar et al., 2011). This interspecific difference in foraging strategy may therefore help explain the different migratory corridors used, rather than species-specific environmental tolerances.

For the spatial prioritisation of conservation management to be successful, migratory routes must be taken into account (Mazor et al., 2016). With these migratory species crossing many international jurisdictions, their conservation is challenging, and requires a diverse and basin-wide collaborative approach to management (Wallace et al., 2011). If marine turtle migratory routes are based on a compromise between minimising energy expenditure and remaining in favourable conditions, the spatial-temporal corridors observed today are likely to alter with climate change. A shift in the prevalence of green turtles migrating from Cyprus to Lake Barawil in Egypt has already been reported (Bradshaw et al., 2017), with a higher proportion of individuals using this route in more recent years. Therefore, conservation strategies must adapt with shifting environmental conditions (Robinson et al., 2009).

4.2 Migratory dives

Minimising energy expenditure during long-distance migrations is paramount. Air-breathing migrants that must surface to breath, can dive to approximately 2.5 times their body thickness to reduce surface drag (Hertel 1966), and likely reduce the influence of wave driven currents, whilst diving substantially deeper than this would likely increase the energetic cost of migration. The loggerhead turtles tracked in this study, however, regularly dived to depths over 5 m, as did the single green turtle with dive data available, and deep migratory dives have been reported in other marine turtle species (e.g. Whiting et al., 2007), as well as other marine vertebrates (e.g. seals, Thompson et al. 1991). Deep dives could provide a sub-surface refuge to reduce predation by preventing silhouetting (Hays et al. 2001a; Thomson et al., 2011). This study shows marine turtles are unlikely conducting deep dives to forage or to remain within thermal tolerances, as herbivorous green turtles would have few prey options, and there was no clear relationship between dive depth and primary production, mixed layer depth, or sea temperature.

The surface drag avoidance theory (Hertel 1966) is only applicable in calm conditions, but marine turtle migrations occur across dynamic seascapes where conditions are changing on relatively fine spatial-temporal scales. This study shows sea state did affect the diving behaviour of loggerhead turtles with larger waves resulting in deeper and longer dives. This provides evidence that diving to 2.5 times their body thickness is not the most optimal migratory option in stormy conditions when turtles retreat to deeper depths. Deeper dives might in fact reduce energy expenditure during high sea states in comparison to travelling near the surface (Hertel, 1966). Surface avoidance behaviour has been reported in hawksbill (Storch et al., 2006) and loggerhead turtles (Sakamoto et al., 1990) during storms to reduce disturbance from wave action. Retreat to deeper waters during storms are also evident for other marine species (e.g. Heupel et al., 2003). Higher frequency of storm events may increase migratory energy expenditure and have carry-over effects (Harrison et al., 2011). However, with a deeper distribution during high sea states, marine turtles may be less vulnerable to anthropogenic activities, such as ship strikes and surface fishing, during storm conditions. Under future climate scenarios, extreme weather events such as storms are expected to increase (Emanuel, 2005; IPCC, 2019), despite this, few studies have directly investigated the effect of wind, waves, or storms on vertical dive behaviours of other air-breathing marine migrants.

Behavioural changes in diving have previously been reported as a response to different temperatures, however, the relationship differs with species and region (Hochscheid, 2014), and is investigated in marine turtles foraging rather than migrating (e.g. McMahon & Hays, 2006; Weir, 2007; Howell et al., 2010). For example, extended surface times related to temperature have been previously reported for foraging loggerhead turtles when solar radiation was highest and was suggested as a basking technique to increase the body temperature of these ectotherms (Hochsheid et al., 2010), whist dive data suggested migrating green turtles do not bask (Hays et al., 1999). Marine mammals (e.g. McIntyre et al., 2011) and penguins (e.g. Culik et al., 2000) are reported to dive deeper for longer in warmer waters when foraging, which was likely due to temperature directly affecting prey distribution. In this study, loggerhead turtles migrated in shallower waters during higher sea surface temperatures. Future increases in sea temperature (IPCC, 2019), may result in an increase in the overlap of marine turtles with surface anthropogenic activities, but shallower dives could also reduce energy expenditure during migrations.

Diel-diving patterns has been reported previously in foraging grounds of marine turtles, for example with turtles moving to different patches dependent on time of day (e.g. Dujon et al., 2018), whilst limited research looks at migratory dives (see Hochsheid, 2014 for review of dive behaviours and references therein). Diel diving patterns are also evident for a large range of taxa (Hays, 2003) and is related to the diel vertical migration of prey, for example, deeper and longer night dives are conducted by several marine mammal species (Scott et al., 2009; Biuw et al., 2010). This study provides evidence for diel-diving patterns in migrating loggerhead turtles with long shallow travel dives evident at night. Previous research suggests diel differences in marine turtle dive behaviour varies between and among species (e.g. Papi et al., 1997; Hays et al., 1999; Rice & Balazs, 2008; Blanco et al., 2012). Shallower night dives in this study were unlikely related to the ability to feed shallower due to vertical migration of prey or due to sea temperature, as the heat flux increases at night, with water losing heat to the atmosphere, and in turn surface waters cool. It may instead be a response to reduced light in the water column, with shallower dives resulting in better visibility.

5. Conclusions

This research demonstrates behavioural plasticity of marine migrants in response to local fine-scale changes in environmental conditions. Movement behaviours of marine species are often used to represent their response to anthropogenic pressures (e.g. Weir, 2007; DeRuiter et al., 2013). This study shows that changes in fine-scale environmental conditions as well as time of day affects dive behaviours. Changes in vertical dive behaviour in response to environmental conditions will affect the susceptibility of migrants to direct anthropogenic pressures and should be taken into consideration within conservation efforts and disturbance studies should either control for these environmental factors or include them in their analysis (Kavanagh et al., 2017). For example, during night-time, calm sea states, and warmer sea temperatures, marine turtles remain in shallow waters making them more susceptible to ship strikes and surface fishing activities such as pelagic longlines. A better understanding of these behavioural changes would enable more spatial and temporally specific conservation measures to be implemented. In addition, shifts in ocean climate could result in both large-scale and fine-scale environmentally driven changes in the migrations of many species. By researching behavioural responses to fine-scale short-term changes, the behavioural alterations documented will inform what may happen under future climate scenarios. Clearly, flexible dynamic ocean management is needed and should be systematically incorporated into conservation decision-making for effective long-term conservation of migratory species.

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Supporting Information

Appendix S1 – Dive profiles

Dives were plotted with the software R 3.5.1 (R Core Team, 2018) and visually assigned as Profile-A, Profile-C, Profile-E, Profile-F, or Other.

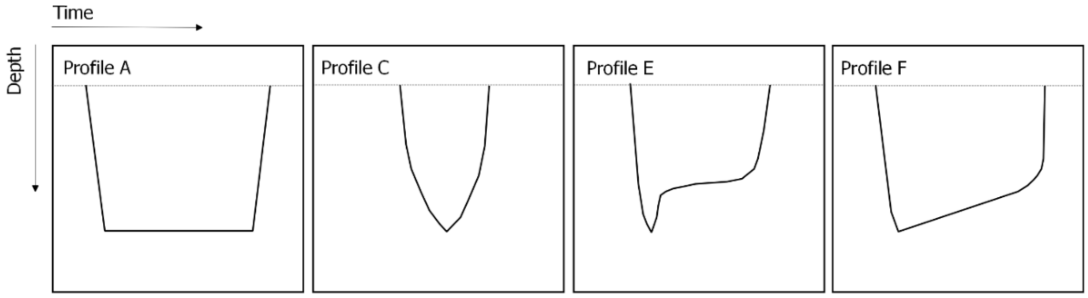

Figure S1.1 Dive profiles performed by loggerhead turtles in this study. The figure does not represent true proportions of depths and dive durations. Adapted from Hochsheid (2014).

Appendix S2 – Migrations

Migrations are thought to be a necessity to move from nesting grounds with inadequate food resources to areas of high food availability (Plotkin 2003). Residential foraging grounds used by both species, suggests long-distance migration is not vital and that sufficient food resources are available in the coastal waters of Cyprus, which are known juvenile foraging grounds (Palmer et al., unpub). Residential foragers and long-distance migrants have been reported within other nesting populations (e.g. Seminoff et al., 2008; Blanco et al.,2012; Esteban et al., 2015; Patel et al., 2015). This raises the question, why do most individuals migrate vast distances, which has significant energetic costs? The various migratory strategies used by a population may be the results of hatchling dispersal by ocean currents (Seminoff et al 2008; Blanco et al., 2012) and could have carry-over effects, with individuals in habitats with low food resources (e.g. residential and oceanic habitats), being smaller in size and in turn may have a lower reproductive output (Hatase et al., 2002; Seminoff et al., 2008). Conversely, residential foragers exclude the need to spend energy on migration and may be able to increase fat reserves and reach reproductive condition quicker than long-distance migrants.

Of the seventy-nine turtles that migrated to distinct foraging grounds, eight loggerhead turtles and three green turtles conducted area restricted search behaviours characteristic of foraging *en route* (lasting for 1 to 11 days). Foraging *en route* was always on the continental shelf for green turtles whilst foraging in the open seas was evident for one loggerhead turtle. For a discussion on foraging *en route* see S3.1.

During coastal migrations both species passed suitable foraging grounds, that are used by other individuals in these nesting populations. Passing known suitable foraging grounds has been seen in other populations (e.g. Blanco et al., 2012) and supports that these nesting populations have high foraging site-fidelity (e.g. Schofield et al., 2010; Haywood et al., 2020).

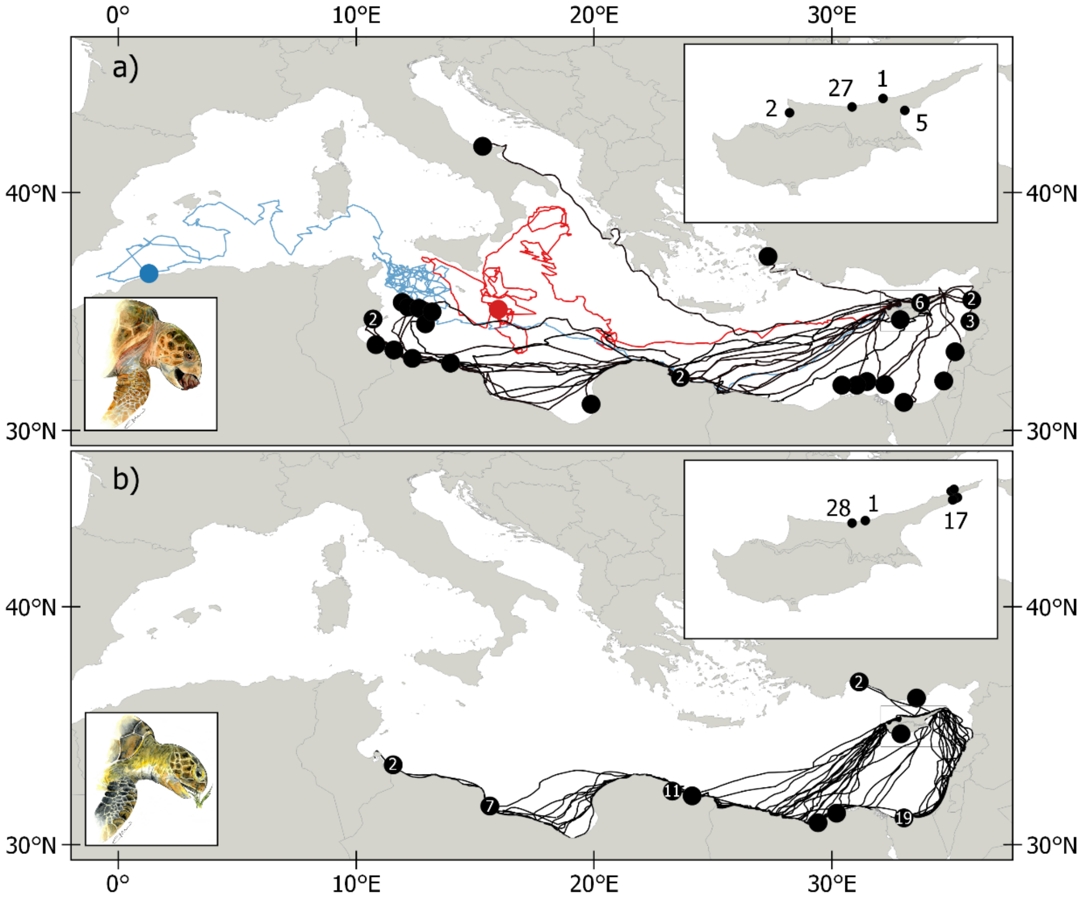

Figure S2.2 Post-nesting migratory routes of a) thirty-five loggerhead and b) forty-six green turtles satellite tracked from nesting beaches in Cyprus. Black lines represent the migratory route and the black circles are the foraging grounds, some of which are numbered as used by multiple individuals. The two loggerhead turtles conducting oceanic foraging are highlighted in red and blue with circles indicating location of termination. Inserts show number of individuals satellite tracked from deployment sites in Cyprus. Artwork inset of a foraging loggerhead and green turtle.

Appendix S3 – Migratory Dives

Appendix S3.1 Foraging en route

Marine turtles are considered capital breeders, fasting during the nesting season, therefore replenishing fat reserves is vital post-nesting (Hamann et al., 2002). In the minority of cases, the use of coastal waters instead of direct migratory routes has been reported and was attributed to allowing refuelling *en route* to final foraging grounds, however, this behaviour was only performed by a few individuals (e.g. Cheng 2000; Dujon et al., 2017). Slower swim speed and area restricted search behaviours in coastal waters have previously been reported in migrating marine turtles, which have been inferred as foraging *en route* (Bentivegna et al., 2007; Cuevas et al., 2008; Seminoff et al., 2008; Baudouin et al., 2015). Therefore, indirect migrations may enable refuelling *en route* which in turn minimises the energetic cost of migration.

In this study, distinct differences were seen in the dive profiles of loggerhead turtles migrating in open seas versus coastal waters. Shallow dives (<5 m) were mostly Profile-C dives and more common in the open seas than coastal waters (20 and 12% of dives, respectively). Of the deeper dives (>5 m) in the open seas the most common dives were Profile-E (39%), followed by Profile-C (25%), and Profile-F dives (24%) whilst few Profile-A dives (5%) were conducted (7% of dives were assigned as 'Other'; Fig 3). The most common dives >5 m in the coastal waters were Profile-E dives (39%), followed by Profile-C (20%), and Profile-A dives (18%) whilst few Profile-F dives (10%) were conducted (13% of dives were assigned as 'Other'; Fig 3). Migratory dives gradually became longer in duration and more Profile-A dives were conducted as an individual approached their foraging ground, suggesting a gradual change in dive behaviour occurs between migration and foraging. For an example of foraging dives see S4 in the Supporting Information. Green turtles swam significantly faster than loggerhead turtles in both coastal (ANOVA, $F_{(1,62)}=36.58$, $p<0.001$) and open seas ($F_{(1,58)}=14.39$, $p<0.001$), which is likely due to green turtles being larger (mean CCL loggerhead=72.87 cm; green=91.86 cm).

Appendix S3.2 Resting en route

In both coastal waters and open seas, the most common dive profile was Profile E (39% of all dives) and these occurred during the day and night (Fig 3). For the Profile-E dives, the gradual ascent phase occurred between 5 and 43 m in depth, regardless of the maximum dive depth, and was not related to the turtle size (GLM: -1.66, p=0.15, n=8). These dives could be resting dives with neutral buoyancy met at the gradual ascent phase during which, swim speeds are slower (Minamikawa et al., 1997), and gliding occurs (Hays et al., 2004). This could provide a sub-surface refuge to reduce predation by preventing silhouetting (Hays et al. 2001a; Thomson et al., 2011). Forward motion still occurs during Profile E dives so migration can continue whilst resting (e.g. Rice & Balazs 2008). To determine whether resting dives occur in specific conditions on-board sensors to determine more accurately the oceanographic conditions during these dives would be required in the future.

On-board animal sensors allow fine-scale oceanographic conditions experienced by an individual to be recorded and directly related to spatial behaviours (Fedak 2004). Satellite derived environmental conditions are often missing in shallow coastal waters, therefore, on-board sensors on marine turtles, which migrate and forage in coastal waters, would help fill these oceanographic data gaps (March et al., 2019; e.g. McMahon et al., 2005). In addition, satellite derived environmental conditions can be used when in situ sampling by PTTs is not available. The present study shows that for this to be successful PTTs need to (1) be designed to minimise the time lag between the turtles location and oceanographic measurements, (2) be calibrated in the laboratory to ensure accurate values are recorded, and (3) the precision and accuracy of the onboard sensors should also be easily available to the consumer (see Appendix S5 in the Supporting Information for a comparison between on-board and satellite sea temperature collected in this study).

Table S3.1 Summary values of female loggerhead and green turtle migratory behaviours in open seas and coastal waters. Dive duration (DD, in hours), surface duration (SD, in hours), maximum dive depth (MD, in meters), and swim speed (SS, in km h^{-1}), n = number of individuals compared.

	Loggerhead					**Green**			
	Location	**Mean**	**SD**	**Range**	**n**	**Mean**	**SD**	**Range**	**n**
DD	Open seas	0.34	0.12	0.01 to 1.28	6	0.25	0.09	0.05 to 0.39	1
	Coastal	0.48	0.14	0.01 to 2.13	6	0.30	0.18	0.03 to 0.64	1
SD	Open seas	0.13	0.03	0.001 to 0.21	6	0.17	0.04	0.05 to 0.20	1
	Coastal	0.10	0.03	0.001 to 0.21	6	0.03	0.007	0.02 to 0.04	1
MD	Open seas	25.7	11.5	4 to 175.5	6	23.2	9.12	12.5 to 59.5	1
	Coastal	32.7	11.9	4 to 147.5	6	13.4	1.96	10.5 to 17.5	1
SS	Open seas	2.03	0.41	0.93 to 2.87	22	2.65	0.38	1.98 to 3.71	42
	Coastal	1.47	0.29	0.76 to 1.86	22	1.87	0.41	0.60 to 2.66	42

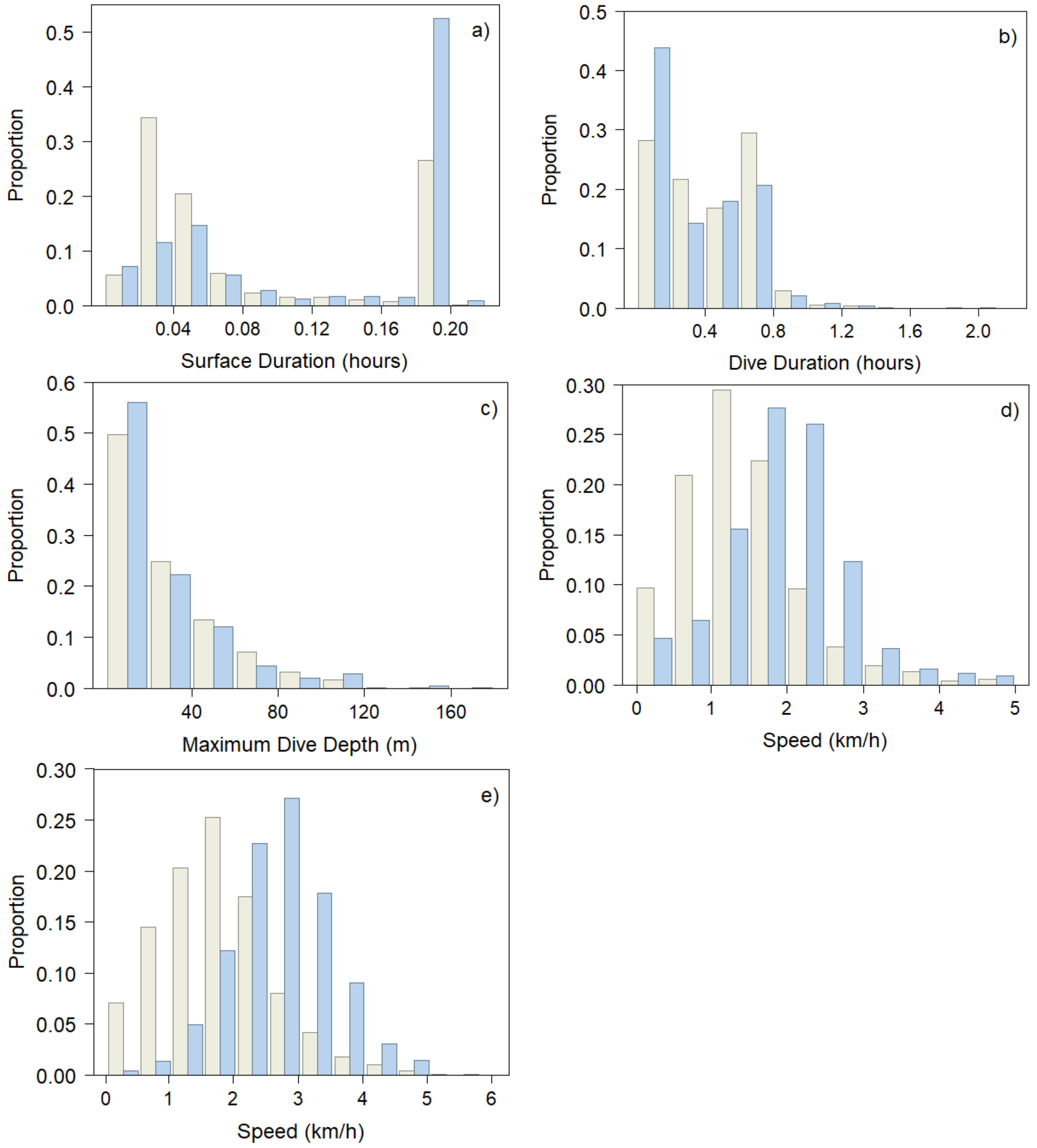

Figure S3.3 Migratory dive behaviours in open seas (blue) and coastal waters (grey) performed by female loggerhead turtles (a-d) and green turtles (e) tracked with SMRU SRDLs from Cyprus. a) Surface duration (n=6), b) Dive duration (n=6), c) Maximum dive depth (n=6), d) loggerhead turtle swim speed (n=22), and e) green turtle swim speed (n=43).

Appendix S4 – Foraging Grounds

Eight loggerhead turtles with SMRU SRDLs reached foraging grounds (whilst one terminated *en route*). Movements within the foraging grounds are defined as ‘residential’ compared to ‘migratory’ and are identified from the state-space models (see Section 2.1 for these methods). Residential movements within foraging grounds were inferred as either foraging or resting, as from locational data alone these behaviours cannot be distinguished (Thums et al., 2017). Profile-A dives were conducted in foraging grounds with individuals rapidly descending to the maximum dive depth where they remained for most of the dive before a rapid and direct ascent (Fig S4.4b). A gradual temporal change in dive behaviour was seen for all individuals with dives of longer duration occurring in colder months (Fig S4.4). The green turtle with a SMRU SRDL conducted short Profile-A and Profile-C dives during warmer months (Fig S4.4d) and long Profile-A dives during the colder months (Fig S4.4e).

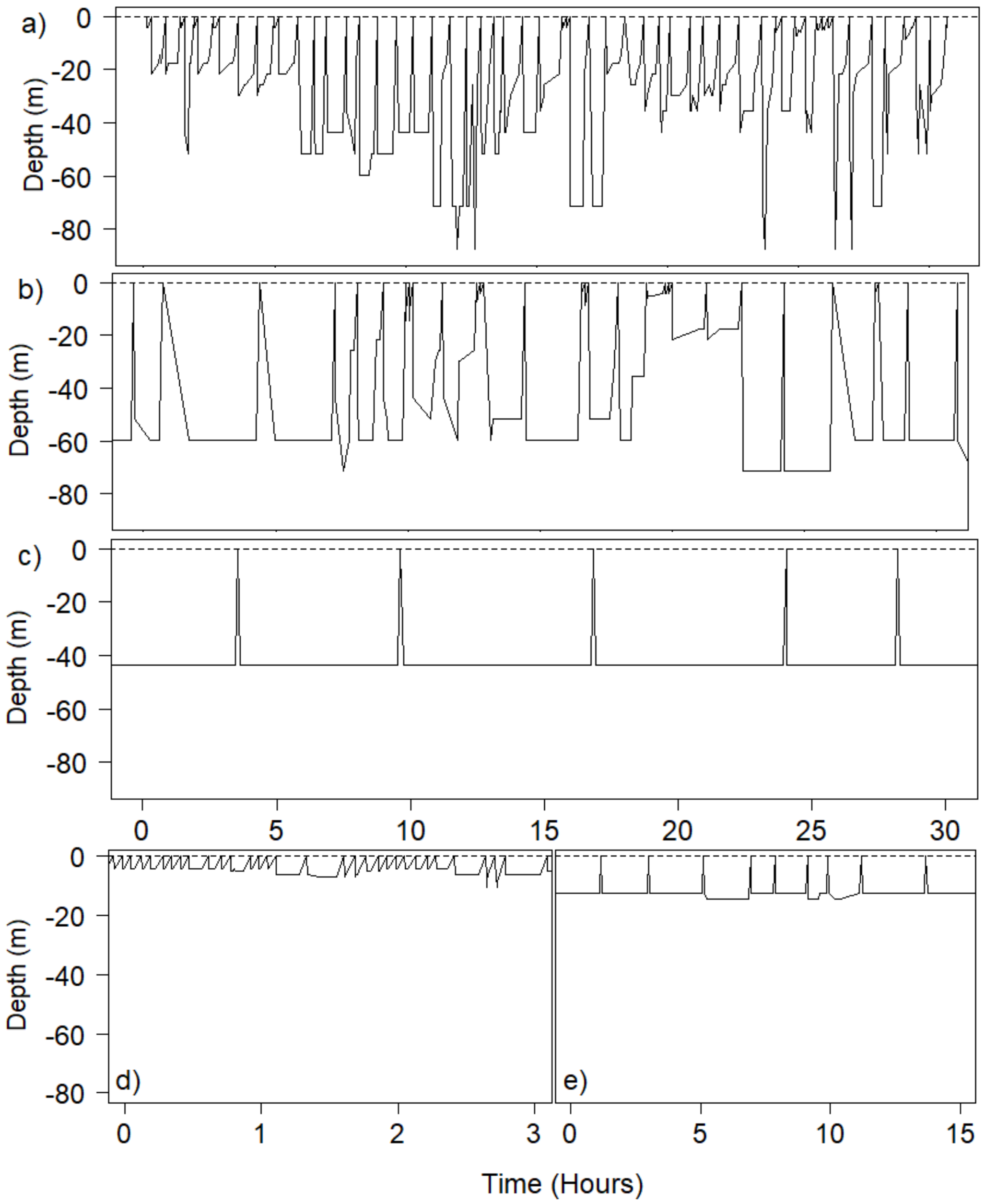

Figure S4.4 Dive profiles of a female loggerhead turtle conducting a) migratory dives, b) foraging ground dives during a warmer month (October), and c) foraging ground dives during a colder month (February). Dive profiles of a female green turtle conducting d) foraging ground dives during warmer months (July-September) and e) foraging ground dives during a colder month (January). Note different x-axis.

To determine if month affected dive behaviours of loggerhead turtles in foraging grounds, GAMMs were used with month set as a cyclic smooth term, PTT set as the random term, and with autocorrelation considered using an ARMA Correlation Structure. In the foraging grounds, dive duration ranged between 0.01 and 10.24 hours. Month significantly affected dive duration, longer dives occurred during colder months (GAMM: F=3.13, edf=3.37, p<0.001, R^2=0.44, n=8, Fig

S4.5a). Neither surface duration (range: 0.01 and 0.20 hours, F=0.66, edf=2.15, p=0.05, R^2=0.10, n=8, Fig S4.5b) nor maximum dive depth was affected by month (range: 4.00 and 95.50 m , F=0.00, edf=0.001, p=0.98, R^2<0.001, n=8, Fig S4.5c).

To determine if dive duration was affected by temporal changes in temperature, dive duration was compared to daily sea surface temperature (Reynolds Optimum Interpolation Sea Surface Temperature data (OISST) available from the NOAA National Climatic Data Center, https://www.ncdc.noaa.gov/oisst). OISST temperature data were used instead of the temperature recorded by the onboard PTT sensors as OISST data gave coverage for all telemetry data (whereas temperature sensor data were only available from some PTTs). The OISST data and PTT data were highly correlated (see Appendix S5 for this comparison), therefore, OISST data is a suitable proxy for the temperature conditions experienced by the turtle. In addition, some PTTs had inaccuracies (see Appendix S5) and therefore OISST data is likely more consistently reliable.

The location of each dive was matched with the temporally closest state-space model output and the temperature was then extracted from this location for that day. Mean daily values were used in the analysis and a GAMM was used with temperature set as the smooth term and PTT as a random term. Turtles dived in sea surface temperatures ranging between 13.7 and 30.5 °C. Temperature significantly affected dive duration, with colder temperatures resulting in longer dive durations (GAMM, F=10.56, p<0.001, Fig S4.5d).

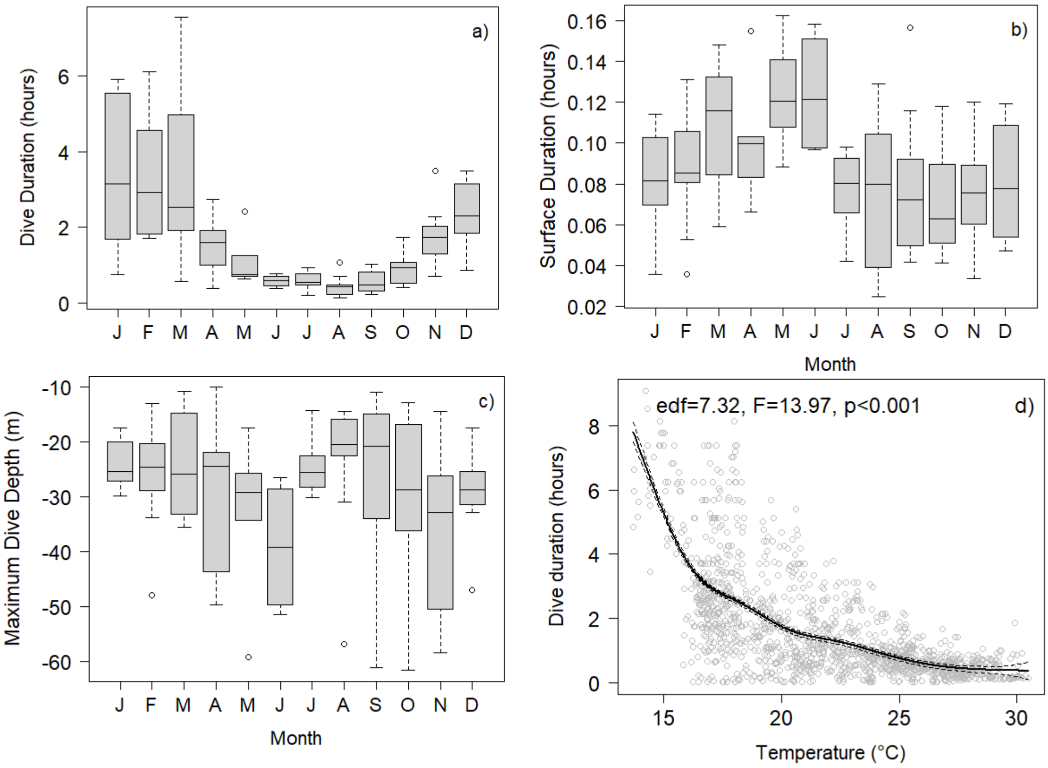

Figure S4.5 Temporal shift in foraging ground dive behaviours of female loggerhead turtles satellite tracked from Cyprus (n= eight turtles). a) dive duration, b) surface duration, and c) maximum depth with month. d) Influence of sea surface temperature on dive duration (n= eight turtles). Solid line represents mean dive duration response and dashed lines represents ± standard error. Edf: estimated degrees of freedom, F: F-statistic, p: significance.

Appendix S5 - Comparison of temperature recorded by two sampling methods: Remotely sensed data and Platform Terminal Transmitters

Daily Reynolds Optimum Interpolation Sea Surface Temperature data (OISST) were available from the NOAA National Climatic Data Center (https://www.ncdc.noaa.gov/oisst). Two Platform Terminal Transmitter (PTT) models recorded temperature, SPOT Wildlife Computers (n = 8) and SMRU SRDLs (n = 6, as temperature data were not available for two PTTs and one PTT terminated before reaching the foraging ground). Wildlife Computers recorded temperature at time of transmission from an internal thermistor resulting in a >15min time lag. For the dives recorded by Wildlife Computers, 34.6 ± 1.03% had temperature measured. SRDLs recorded temperature at twelve depths during a dive from which the surface temperature value (recorded at 5 or 6 decibars) was selected for further analysis. Of all SRDLs dives recorded, 4.43 ± 1.51% had temperature measured and 41% of dives were removed from the analysis for SRDLs due to an error reading of 35.95 °C. For both PTT models, the location that the PTT temperature was recorded was determined as the temporally closest state-space model output. The temporally closest OISST data point was then extracted for this location. Only values recorded in foraging grounds were used, whilst migratory values were not included.

Although temperature significantly differed between OISST and PTTs for both PTT models (GLMM, Wildlife Computers, $t=4.26$, $p<0.001$; SRDLs, $t=-2.10$, $p=0.03$), there was a significant correlation between temperature recorded by OISST and both Wildlife Computers (Spearman's correlation, $p<0.001$, rho=0.93) and SRDLs ($p<0.001$, rho=0.57). When each PTT was considered separately, temperatures from all Wildlife Computers were significantly correlated to the OISST ($p<0.001$) but only four of the six SRDLs were significantly correlated ($p<0.001$, Fig S5.6). This was due to two SRDLs recording a large range of temperatures in comparison to the OISST as well as all other PTTs (Fig S5.6). When these SRDLs were removed from the analysis the strength of association was drastically increased for SRDLs (Spearman's correlation, $p<0.001$, rho=0.94).

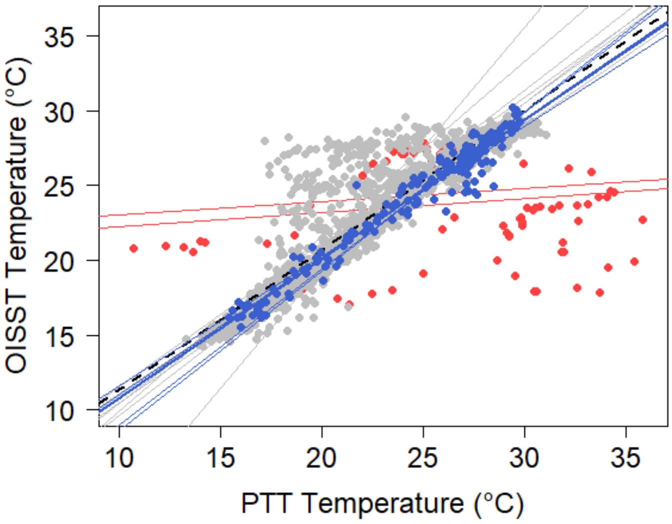

Figure S5.6 Comparison of temperature recorded from Platform Terminal Transmitters (PTT) deployed on female loggerhead turtles in Cyprus and from remotely sensed data (OISST). SPOT Wildlife Computers (n = 8, grey), correlated SMRU SRDLs (n = 4, blue), and uncorrelated SMRU SRDLs (n = 2, red). Faint lines = linear regression of each PTT, dashed black line = overall regression for Wildlife Computers, solid blue line = overall regression for correlated SMRU SRDLs.

Highly correlated but different temperature values are expected to be recorded between OISST and PTTs due to differences in the sampling methods. Wildlife computers have a >15 min time lag between location and temperature measurements, therefore, the temperature of the PTT at transmission represents water temperatures previously experienced at varying depths. The shallowest temperature measure available for the SRDLs was recorded at five or six decibars. In comparison, remote satellite sensors are recording daily values and are observing the upper 1-10 mm of the sea surface, which is influenced by sea-air heat fluxes. In addition, the observed difference may be due to solar heating of the PTTs during surfacing events (e.g. Bahr et al. 2016; Brewin et al. 2020). SRDLs outputted 35.95 °C as an error value and this may be due to insolation during basking events raising the PTT temperature. This has been previously reported by March et al. (*2020 in prep*). However, in this case the surface duration of foraging dives ranged between 1 to 10 minutes and the PTT temperature values were lower than OISST values.

Only 35 and 5% of dives had associated temperature values for Wildlife Computers and SRDLs, respectively. This is likely due to various factors affecting the amount of recovered data, including; the repetition rate of the PTT (determining the frequency of messages sent to ARGOS), the proportion of messages with temperature values, the duty cycle of the PTTs, the ARGOS coverage, and the behaviour of the turtles with extended surface duration resulting in an increase in messages sent.

Appendix S6 – Chlorophyll-a Concentration

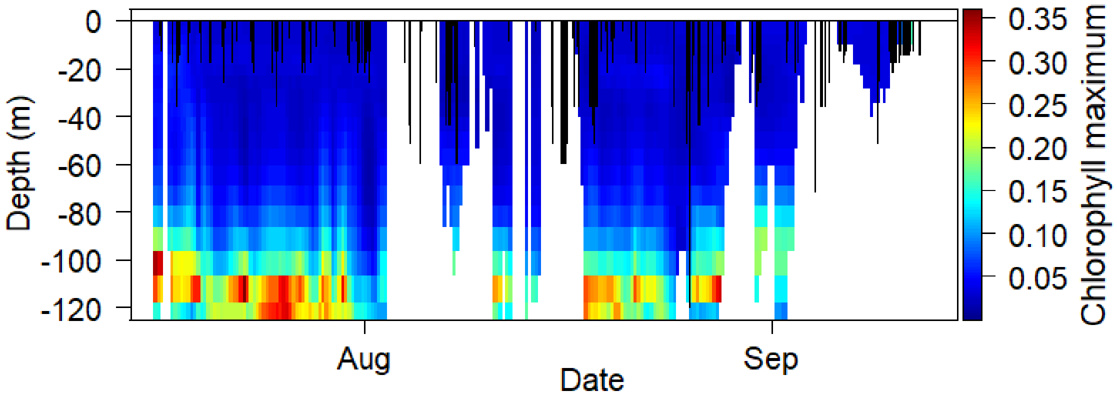

Figure S6.7 Migratory dives of Turtle_4206 deployed with a SMRU SRDL from Cyprus overlaid on chlorophyll-a concentration (in milligram m^{-3}). White sections are locations or depths without chlorophyll data.

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CHAPTER 6: GENERAL DISCUSSION

This research provides new information on the spatial and foraging ecology of Mediterranean marine turtles and demonstrates how these methods could be applied to other marine migrants. I show that juvenile loggerhead turtles follow different developmental strategies dependent on region, that a shift in habitat and prey occurs with size, and I emphasise the importance of region-specific and habitat-specific conservation to protect this vital life phase. I identify key foraging regions in the Mediterranean for adult loggerhead turtles to help inform targeted conservation. Finally, I demonstrate that species-specific migratory routes are likely dependent on the physiology of a species, that vertical migratory dive behaviours are affected by changes in environmental conditions, and that dynamic conservation plans that can shift with future changes in the ocean climate must be implemented.

1. Spatial and foraging ecology

Mediterranean marine turtles face major threats within the marine realm (Casale et al., 2018). Despite this, conservation and conservation-driven research has historically been targeted to the easily accessible nesting grounds (Hamann et al., 2010). Nest counts in Mediterranean rookeries are not increasing as rapidly as expected in spite of intensive conservation efforts on the nesting beaches. This may be a result of lack of protection away from the nesting beach, where the majority of their life cycle occurs, and requires alternative conservation approaches to be considered (Casale et al., 2018). With individuals travelling vast distances between breeding and foraging grounds, understanding their distribution and habitat use in the marine realm is challenging and has resulted in large knowledge gaps in their marine spatial ecology.

In **Chapter 2**, I demonstrated how stable isotope analysis (SIA) is a powerful tool for investigating the marine spatial ecology of marine turtles, and by conducting an exhaustive study of peer-reviewed literature, demonstrated the wealth of ecological information gained. By summarising current knowledge obtained from SIA, **Chapter 2** explored the considerable flexibility and ecological complexity of the life histories of marine turtles, demonstrating that SIA may help reveal the cryptic diet of many species and indicate diet variability between foraging sites, so that critical habitats important for foraging populations are protected (e.g. Reich et al., 2007; Ramirez et al., 2015). In addition, this review demonstrated how SIA can inform conservation initiatives by identifying threats faced (e.g. Agusa et al., 2011), and providing pre- and post-disaster information by investigating whether the spatial ecology of individuals shift with unfavourable conditions (e.g. Vander Zanden et al., 2016, Reich et al., 2017). Isotope ratios were summarised at a global scale and demonstrated intraspecific regional differences and interspecific overlap. The review highlighted the geographical gaps in the current knowledge, the bias in the species studied, and provided a comprehensive list of recommendations that helped inform subsequent chapters and would be applicable to other marine migrant studies. This work also provided an inventory of all published marine turtle stable isotope studies, summarised in an open access inventory to enable researchers to add new studies and target future work. The benefits of SIA were further proven by its use in **Chapter 3** and **Chapter 4** to investigate the spatial and foraging ecology of juvenile and adult Mediterranean marine turtles.

1.1 Juvenile ecology

Marine turtles have complex life-history patterns, utilising a wide range of ecosystems throughout their life cycle and facing various natural and anthropogenic threats at each life stage (Bolten, 2003). In the Mediterranean, loggerhead turtles have been reported to follow alternative life-history patterns and intra-population differences in habitat use are also reported (Casale et al., 2008, 2015). To better understand fisheries interactions and for successful conservation of loggerhead turtle populations, it is necessary to understand inter- and intra-population variations in habitats used and resources exploited (Hamann et al., 2010; Rees et al., 2016). **Chapter 3** showed juveniles had different isotope ratios dependent on geographical region, suggesting different habitats are being used by each population, and providing support for differing life strategies in the Mediterranean. For example, in regions such as Amvrakikos Gulf (Greece), the NE Adriatic, and Cyprus, juveniles had isotope ratios suggestive of foraging predominantly in neritic habitats. This is supported by stomach contents of stranded turtles from these regions showing a diet dominated by benthic prey items (Lazar et al., 2008a, b). In comparison, where oceanic and neritic habitats are available, such as the Central Mediterranean, juveniles had isotope ratios characteristic of foraging in a more oceanic habitat. Diets reported in this region consisted of both benthic and pelagic prey items (Casale et al., 2008). Inter- and intrapopulation differences in foraging strategies have been reported in other ocean basins, for example Pacific loggerhead turtles may become neritic or remain oceanic foragers (Hatase et al., 2002).

In addition, we reported that intra-regional variation in spatial and foraging ecology differed with size but not sex. Size-structured trophic ecology within sharks has been highlighted using SIA (Bird et al., 2018). In the predominately neritic habitats, it was likely that larger individuals with increased diving capabilities (Salmon et al., 2004; Marshall et al., 2012), consumed larger numbers of higher trophic prey from neritic sources. This isotope ratio and size trend has been reported for juveniles undertaking oceanic–neritic ontogenetic shifts in other ocean basins (e.g. Snover et al., 2010; Ramirez et al., 2015; Turner Tomaszewicz et al., 2017). The shift reported in **Chapter 3** is supported by the fact that in these neritic habitats, where bottom-set fishing gear is used, larger individuals are more frequently encountered (e.g. Rees et al., 2013; Snape et al., 2013). This supports the traditional ontogenetic life-history model of a distinct shift in preference from oceanic to neritic habitat use with increased size (Musick and Limpus, 1997). In comparison, no size-related shifts were evident in regions where oceanic and neritic habitats were available suggesting juveniles use these habitats interchangeably, which has been previously reported in other ocean basins (e.g. Revelles et al., 2007; Clusa et al., 2016; Piovana et al., 2020). This challenges the traditional life-history model and has been previously reported for the Central and Western Mediterranean where juveniles as small as 0.25 m (CCL) start to utilise both neritic and oceanic habitats interchangeably (e.g. Casale et al., 2008; Lazar et al., 2008a).

1.2 Adult ecology

Adult marine turtles make cyclic reproductive migrations between distant foraging and nesting grounds (e.g. Shillinger et al., 2008) and several geographically distinct foraging areas are typically used by individual nesting populations (Seminoff et al., 2008; Stokes et al., 2015). A lack of knowledge of where and how populations move throughout their distribution makes it difficult to identify potential risks to their survival. It is therefore necessary to identify critical habitats and understand the geographical range and migratory connectivity of a species for successful development of long-term conservation plans (Webster et al., 2002) and is considered a research priority in Mediterranean marine turtle ecology (Casale et al., 2018).

The findings of **Chapter 4** and **Chapter 5** greatly enhanced our understanding of the movements and habitat use of adult loggerhead and green turtles in the Mediterranean. In **Chapter 4**, satellite telemetry and SIA were used to present a more comprehensive picture of where adult Mediterranean loggerhead turtles are foraging. This was the first study to analyse carbon, nitrogen, and sulphur isotopes for loggerhead turtles in the Mediterranean, confirming the importance of the Tunisian Plateau as a critical habitat for two major loggerhead turtle rookeries. This region has been highlighted as important for male (e.g. Casale et al., 2013; Schofield et al., 2013) and juvenile loggerhead turtles (Casale et al., 2012) as well as other rookeries (e.g. Hays et al., 2010; Schofield et al., 2013). The results of **Chapter 4** suggest foraging ground fidelity occurs in loggerhead turtles, which supports previous research in other ocean basins, including the Indian Ocean (Thomson et al., 2012) and the Gulf of Mexico (Vander Zanden et al., 2016). SIA can also be used to infer foraging site fidelity in marine mammals (Schell et al., 1989; Newsome et al., 2010).

By conducting SIA on a long-term individual-based monitoring programme, this was the first study to show foraging ground fidelity for up to five nesting seasons. **Chapter 4** was also the first study to determine how each foraging ground contributes to a nesting cohort over multiple decades, showing that the foraging grounds in the Mediterranean persist on a decadal-scale, which may indicate that recruitment, survivorship, and conditions potentially remain similar in these regions. This differs from major Atlantic populations, where significant shifts in the relative contributions to foraging grounds have been reported (Vander Zanden et al., 2014; Ceriani et al., 2017).

1.3 Influence of environmental conditions on spatial ecology

Marine migrants are considered especially vulnerable to climate change, with shifts in ocean climate likely affecting their spatial ecology (Robinson et al., 2009; Lascelles et al., 2014). The environmental conditions that they experience during migration differ both spatially and temporally, yet how they respond to these changes has received little attention. To effectively protect marine migrants, we need to not only know their distribution (as investigated in **Chapter 3** and **Chapter 4**) but also how they interact with, and are influenced by, the dynamic marine environment (Luschi et al., 2003; Jeffers & Godley, 2016). Limited research has investigated the influence of oceanographic conditions on marine turtle behaviour, particularly during migrations (Hochscheid, 2014; Hays et al., 2020). **Chapter 5** evaluates the influence of environmental data on the migratory corridors and dive behaviour of two sympatric Mediterranean turtle species. This is the first study to investigate how the vertical migratory dive behaviour of marine turtles is affected by sea temperature and sea state. **Chapter 5** demonstrated behavioural plasticity of Mediterranean loggerhead and green turtles in response to local fine-scale changes in environmental conditions. During night-time, calm sea states, and warmer sea temperatures, loggerhead turtles remain in shallow waters. Surface avoidance behaviour, of longer deeper dives, was recorded during high sea states, which has been previously reported for loggerhead turtles (Crowe et al., 2020) and sharks (Heupel et al., 2003). **Chapter 5** also shows that the species-specific migratory corridors have similar environmental properties (magnetic field intensity, sea temperature, thermal fronts, surface geostrophic and Ekman currents, and wind), suggesting both species may follow similar cues. The species-specific migratory routes taken may therefore be dependent on the physiology and foraging strategy of each species, with green turtles undertaking a more direct route to the coast where they can forage whilst loggerhead turtles remain in the open sea for longer, where oceanic foraging can occur. Migratory routes are also likely a compromise between reducing migratory distance, minimising time from foraging, minimising swimming effort, whilst attempting to remain in favourable conditions by staying in warmer sea temperatures.

2. Implications for conservation

In the Mediterranean Sea, bycatch is one of the key threats to marine turtles resulting in high levels of mortality in both neritic and oceanic habitats (Casale, 2011; Casale et al., 2018). Within the Mediterranean, fishing gear and intensity are region and habitat specific, so the susceptibility of marine turtles differs according to inter- and intra-population variations in spatial and foraging ecology (Casale, 2011). SIA has been used globally to demonstrate size-related variation differences in habitat use for loggerhead turtles and in turn highlighting the need for conservation management to consider population sub-groups (e.g. Hatase et al., 2002; McClellan et al., 2010; Snover et al., 2010; Thomson et al., 2012; Ramirez et al., 2015; Turner Tomaszewicz et al., 2017). The findings of **Chapter 3** show juveniles among and within regions have differing spatial ecology and therefore may have varying susceptibility to different fisheries. Turtles in neritic habitats will become more susceptible to bottom set gears as they grow larger. In comparison, those using oceanic and neritic habitats interchangeably will be susceptible to both bottom set gears and pelagic long lines throughout their size range (Casale, 2011). Region and habitat use will also likely affect their susceptibility to other anthropogenic threats such as the ingestion of debris and chemical pollution (Franzellitti et al., 2004; Casale et al., 2008, 2016). Therefore, the results of **Chapter 3** suggest region-specific and habitat-specific management approaches are required within the Mediterranean to protect juvenile marine turtles.

Chapter 4 identified the Tunisian Plateau as a critical habitat for Mediterranean loggerhead turtles and therefore recommended this relatively small region, as a potential area for future site-specific conservation strategies and fisheries management. Protecting this region may dramatically increase the survival of individuals in this foraging ground and aid in the recovery of many loggerhead rookeries across the Mediterranean. By conducting the study across 25 years, the longest study of its kind, I demonstrate that loggerhead turtles show foraging site fidelity and foraging grounds are persistent across decades. This enables temporal shifts in relative importance of foraging grounds to be assessed, enabling adaptive conservation management. These results provide baselines to develop and assess future conservation strategies.

With changes in environmental conditions altering vertical migratory dive behaviours, as reported in **Chapter 5**, the susceptibility of migrants to direct anthropogenic pressures, such as ship strikes and fishing activities, may change and should be taken into consideration within conservation efforts. In addition, with sea temperature and extreme weather events such as storms expected to increase with climate change (Emanuel, 2005; IPCC, 2019), turtle migrations may be more energetically demanding as individuals engage surface avoidance behaviours, diving deeper for longer, to avoid high sea states. Surface avoidance has been reported previously in marine turtles during storms to reduce disturbance from wave action (Sakamoto et al., 1990; Storch et al., 2006). A better understanding of these behavioural changes would enable more spatial and temporally specific conservation measures to be implemented and could represent what may happen under future climate scenarios. In addition, movement behaviours of marine species are often used to represent their response to anthropogenic pressures (e.g. Weir, 2007; DeRuiter et al., 2013), and with **Chapter 5** showing that environmental conditions affect the vertical movements of marine turtles, disturbance studies should either control for these environmental factors or include them in their analysis (Kavanagh et al., 2017).

Shifts in the ocean current regimes are likely with future climate scenarios (Hoegh-Guldberg & Bruno, 2010), which could displace marine migrants, affect navigation to final destinations, and increase the energetic demands of migration, however, **Chapter 5** shows marine turtles often travel against surface currents with little effect on their migrations, which has also been previously documented (e.g. Bentivegna et al., 2007; Cuevas et al., 2008). Shifts in sea temperature, are expected to continue to change under future climates (IPCC, 2019), and have been reported to cause range shifts in marine turtles (e.g. McMahon & Hays, 2006). With **Chapter 5** demonstrating that migratory routes are potentially selected based on thermal tolerances, the spatial-temporal corridors observed today are likely to alter along with climate change. Therefore, flexible dynamic ocean management is needed and should be systematically incorporated into conservation decision-making for effective long-term conservation of migratory species.

3. Future work

The research within this thesis concentrates on the spatial and foraging ecology of juvenile and adult marine turtles. Leading on from this research and to better understand the spatial ecology of marine turtles, two ideas are proposed for future work.

As shown in **Chapter 5**, marine turtles alter their behaviours in response to local, fine-scale changes in environmental conditions and suggests that the migrations of marine turtles may follow large-scale environmental cues. Under future climate scenarios, sea temperatures are likely to continue increasing, and extreme weather events are expected to change in frequency but increase in strength (IPCC, 2019), resulting in shifts in ocean circulation (Hoegh-Guldberg & Bruno, 2010; IPCC, 2019). Therefore, how environmental conditions and future changes in ocean climate may influence marine turtle spatial ecology is important to enable more effective long-term conservation plans and should to be considered in future work.

3.1. Hatchling dispersal, survival and fate

Surface currents in the global oceans are thought to passively disperse marine turtle hatchlings to the foraging grounds which they then return to throughout their lifetime (Hays et al., 2010; Putman et al., 2012; Scott et al., 2012; Casale and Mariani, 2014). To date, particle drift models for the Mediterranean suggest the east Mediterranean basin and the Adriatic Sea as potential oceanic nursery habitats (Casale & Mariani, 2014; reviewed in Casale et al., 2018). Temporal differences in hatchling dispersal have been simulated and are thought to be due to variations in surface currents (e.g., Hays et al., 2010). With shifts in ocean circulation likely with future climate scenarios (Hoegh-Guldberg & Bruno, 2010), shifts in hatchling dispersal and in turn adult foraging grounds may occur (Hays et al., 2010). Previous particle drift models used thermohaline, geostrophic, and Ekman currents to predict the dispersal of hatchlings (e.g. Hays et al., 2010; Casale & Mariani, 2014). However, for a more realistic representation of hatchling dispersal and survival, investigating their drift patterns in response to a more complete surface current description that includes geostrophic, Ekman, wave driven orbital currents (Stokes drift), and tides is required. This will enable future hatchling dispersal studies to investigate how shifts in oceanographic conditions, for example storm events, affect hatchling dispersal and survival, to better understand what may happen under future climate.

Preliminary work on this has been conducted using particle drift models. To determine where loggerhead turtle hatchlings disperse to, their survival rate and possible fate, virtual particles were released from the major Mediterranean nesting beaches (see Fig 2 in Chapter 1) across the hatchling season (1st August to 30th September, 2014 and 2015) using a particle modelling framework (e.g. Lacerda et al., 2019). Daily horizontal velocities of geostrophic and Ekman currents as well as Stokes drift for surface waters were included in the model runs using satellite and model re-analysis data. Simulations were run for 12 months since the first particle was released. Separate annual simulations were run for two decades (nesting seasons in 1995 to 2015) to determine if temporal shifts in ocean circulation affects hatchling dispersal and survival. Several models were run to investigate the influence of 1) advecting all particles offshore that hit land versus stranding those that hit land (to simulate that hatchings survival could decrease by wave interactions with the coast or where strong currents persistently force them ashore), and 2) not including versus including Stokes drift in the model (to determine how Stokes drift influences hatchling dispersal). Preliminary results show that 1) models stranding particles that hit land removes up to 99% of particles and distinct differences between hatchling dispersal where evident (suggesting hatchlings are capable of actively orientating away from the coast), 2) dispersal differs annually (due to oceanographic conditions and therefore storms may affect hatchling dispersal), and 3) the Levantine basin may be an important nursery ground (Fig 1).

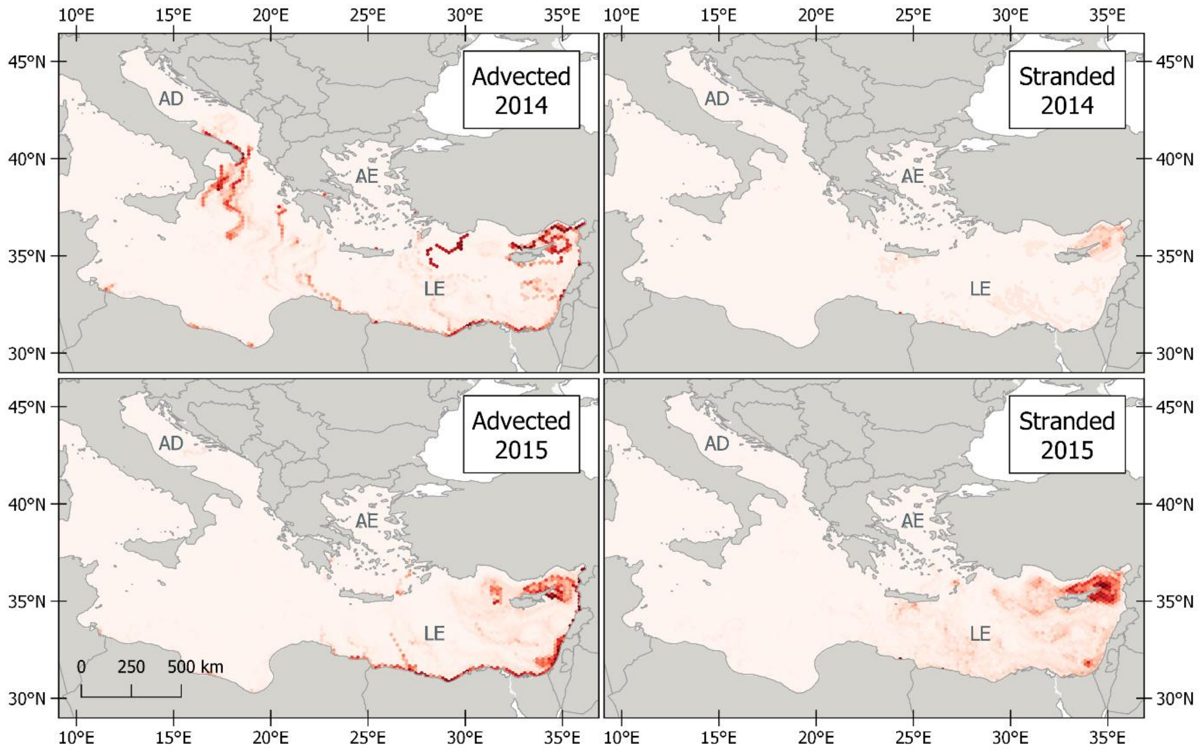

Figure 1. Dispersal of loggerhead turtle hatchlings across the Mediterranean modelled using particle drift analysis. Models were able to either advect particles offshore when the particle interacted with the coastline (first column) or able to strand particles on the coast (second column). Models were run in 2014 (first row) and 2015 (second row). Ad = Adriatic Sea, AE = Aegean Sea, LE = Levantine Sea.

3.2 Enabling the use of Animal borne environmental sensors for Earth system science

Oceans have absorbed >90% of anthropogenic heat since the industrial period (Zanna et al., 2019), but the heat content varies with depth and the Mediterranean heat content was not analysed, presumably due to a lack of temperature observations. To help monitor heat fluxes within the surface and interior ocean, more observations are required. Recent work has suggested the use of animal-borne instruments to complement global ocean observing systems, with animals able to sample areas that are currently not covered by ocean observing systems (March et al., 2019).

In **Chapter 5**, a comparison between the temperature recorded by remotely sensed data and platform Terminal Transmitters (PTTs) was conducted. This highlighted several issues that need to be overcome before the PTT measurements can be thoroughly exploited for Earth system science, including; >15 min time lag between the temperature being sampled and recorded, 41% of dives recorded by SMRU SRDLs had unexplained temperature sensor failures sporadically throughout deployments, a lack of temperature sensor characterisation prior to deployment and no understanding of sensor temporal drift due to biofouling or sensor age. The issue of a lack of characterisation means that no uncertainty information is available for these sensors and no standard quality control procedures appear to exist. As a result, the PTTs deployed during this research have limited use for Earth system science. This can be improved upon in the future, for example, the manufacturers providing specifics about the sensor used, including its associated uncertainty information, the characterisation of each temperature sensor in a water bath prior to deployment (e.g. Brewin et al., 2015), as well as a community-wide effort to agree and develop standard temperature data quality control procedures and protocols for these sensors. This relatively small additional effort would significantly enhance the benefits of these data and sensors to the Earth system science community. The work in **Chapter 5** shows that some of the historical PTT temperature measurements could be utilised for Earth system science applications if quality control procedures were used. Understanding these issues may also provide insight into how to improve the quality of all measurements taken by the PTT tags.

CONCLUSION

The research within this thesis 'The spatial ecology of Mediterranean marine turtles: insights from stable isotope analysis, satellite telemetry, and environmental observations' has enhanced our understanding of the movements and habitat use of juvenile and adult loggerhead and green turtles in the Mediterranean. It highlighted the range of complex developmental strategies used by juveniles and provided evidence for the need of region-specific and habitat-specific strategies to protect this vital life phase. This research identified critical marine habitats used by adults where conservation should be targeted, it demonstrated that migrations are affected by changes in environmental conditions, and supports the need for dynamic conservation plans that can shift with future changes in the ocean climate.

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